COLOR DISCRIMINATION AND COLOR-OPPONENT STRENGTH IN NORMAL, PROTAN, AND DEUTAN OBSERVERS

By

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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Observers made Rayleigh matches and bichromatic mixture threshold judgements at four different field sizes to explore how the size of the color stimulus affects the relationships between color discrimination and color-opponent strength. All subjects were screened with the Farnsworth-Munsell 100 Hue Test. The sample of 25 observers included 6 color-normals, 8 protans, and 11 deutans. Each subject made 5 Rayleigh matches and 3 bichromatic mixture thresholds with .38, .75, 1.5, and 3.0 degree fields. The Rayleigh matches (index of color discrimination) and mixture thresholds (index of color-opponent strength) were correlated. Between-group comparisons were made using analyses of variance.

Color discrimination and color-opponent strength were positively correlated (r^2 = .55) as expected. Color-normal observers with good color discrimination on the FM-100 had strong color-opponency at all field sizes while those with poor discrimination had weaker color-opponency overall, and very weak opponency when tested with the smallest field. Among color-normals, color-opponent strength increased as the test field was enlarged. Dichromats, who had no color discrimination at any field size, showed no evidence of color-opponent processing at any field size. Both extreme and simple anomalous observers showed improvements in color discrimination with increases in field size. Extreme anomalous observers showed very little opponency at any field size, while simple anomalous showed evidence of a modest amount of color-opponency at the larger field sizes. Analyses of variance showed that both color discrimination and color-opponent strength were significantly different for all comparisons made between normal, extreme, and simple anomalous observers.

Differences in luminance additivity among simple vs. extreme anomalous may indicate that different processes underlie color-opponency for these observers. The findings on color-normal observers revealed an analagous difference for good vs. poor color discrimination among color-normals.

CHAPTER 1

INTRODUCTION

Our perception of the world around us is shaped by our sensory interactions with it. For most animals, including man, vision is an important sensory dimension which is used to impart visual qualities such as size, motion, depth, and color to the world. Our visual perceptions have their basis in features of the physical stimulus, but are also products of the visual system which is used to view them.

There is a tremendous amount of diversity in the types of visual systems found in the animal kingdom. In many species visual systems are specialized, and some visual capabilities are reduced or sacrificed in order to enhance others, presumably as a selective adaptation to the animal's visual enviroment (Hughes, 1973; Walls, 1942). For example, visual acuity is sacrificed in nocturnal eyes specialized for sensitivity, or binocular overlap is sacrificed for greater field of view in lateral-eyed prey species.

This diversity seems to be especially true for the visual sensation of color, the ability to discriminate between lights which differ in their wavelength

composition. Three things about color vision make it notably different. First, color vision differs a great deal between species. Compared to humans, some species possess very good color vision, others very poor, but the more or less discriminating color vision sub-types can be found in most phyla (Jacobs,1981; Walls, 1942). Secondly, color vision seems to be associated with a great deal of variation within species. Some animals in a given population may enjoy a quality of color vision much different than that of others. Some of this variation is due to normal genetic variation via the inheritance of different alleles of the genes that determine color vision. This is the case in some species of new-world monkeys, where there are as many as 6 sub-groups of individuals with different color vision. Each sub-group is normally occurring in the population with a known frequency (Jacobs & Neitz, 1987). It appears this may be true of humans as well, as discussed below. Lastly, this variation in color vision seems to be very prone to abnormal genetic variation, including both the inheritance of defective genes and recombinative alterations during genetic transcription. This also is true in humans; 8-10% of the male population have inherited color vision defects (Kalmus, 1965; see also below).

Inherited defects of human color vision differ from normal color vision in characteristic and predictible

ways. The present study is one designed to help understand these differences. First consider the normal processing of color information which, very generally, is based on two important visual processes: the transduction of light by different cone photopigments and the color-opponent neural processing of these cone signals.

Normal Human Color Vision Relies on Three Normal Cone Photopigments

Normal human color vision relies on three cone photopigments which are maximally sensitive to lights from different parts of the visible spectrum. For lights measured at the cornea, the maxima of the spectral sensitivities of these pigments lay near 440, 550 and 570nm for the short wavelength sensitive (SWS), middle wavelength sensitive (MWS), and long wavelength sensitive (LWS) cone photopigments respectively. Since the relative absorption of these pigments varies as a function of wavelength, lights of different wavelength compositions can result in different amounts of activity in the three cone types. This idea of color being coded by three cone channels is known as the "Trichromatic Theory" of color vision (Helmholtz, 1866/1962). Color vision based on these three pigments results in excellent wavelength discrimination. The color-normal just noticeable difference for a change in wavelengths is less than 2 nanometers across most of the visible spectrum. However, color vision based on these three pigments also results in

the inability to make color discriminations among some lights of multi-wavelength composition (e.g. metamerism).

Color-normal individuals who possess all three pigments and are free from other visual problems are trichromatic. Color-normal individuals require at most a mixture of 3 wavelengths of light to match the color of a single wavelength in the visible spectrum. These color matches can be predicted by solving colorimetric equations that relate the amount of energy at each wavelength of light to the quantal efficiencies for absorbtion by the three cone photopigments. A color match is achieved between different lights when the quantal absorbtions by all three photopigments have been equated for the different lights.

Normal Color Vision May Include Distinct Sub-Types

Several studies over the years have questioned whether there may exist subtle variations in normal color vision that are based on small individual differences in the spectral sensitivities of the photopigments. Psychophysical studies (Alpern & Wake, 1977; Wald, 1966) and physiological (microspectrophotometry) (Alpern & Wake, 1977; Dartnall et al., 1983) studies of the LWS and MWS photopigments have frequently reported differences between individuals in the peak spectral sensitivity for these two photopigments. These findings were often viewed with some skepticism because of the difficulty in ruling out other

factors such as measurement error and pre-retinal absorbtion. The studies cited above controlled for these factors.

Twenty years ago Waaler (as cited in Mollon, 1986) reported finding individual differences in a commonly used color matching task. The large sample of men he tested performed this task in such a way that he concluded that there must be more than the two traditional MWS and LWS photopigments in the color-normal eye. This did not gain wide acceptance at the time. Currently researchers are re-investigating the possibility that there may be bimodalities in large sample color match data. A recent study has also reported finding a bimodality in these matches similar to that reported by Waaler, and it is believed to be due to individual differences in the LWS cone pigment (Neitz & Jacobs, 1986). In the Neitz and Jacobs study subjects behaved as if they possessed one of two (and possibly three) LWS cone pigments that differed in peak spectral sensitivity by approximately 3 nanometers. This study has been replicated and extended by the authors (Deegan, Neitz, & Jacobs,1989; Neitz & Jacobs, 1988; Neitz & Jacobs, 1990). Other researchers have failed to find this difference (Jordan & Mollon, 1988; Lutze, Smith, & Pokorny, 1990; Woods & White, 1990), but this may be because it requires an unconventional technique to reveal them.

Protan and Deutan Forms of Abnormal Color Vision Result From Missing or Spectrally-Shifted Photopigments

Approximately 8-10% of the male population have red/green color vision problems because of inherited photopigment defects. These defects fall into two general categories: those defects resulting from the inheritance of a photopigment with unusual spectral sensitivity and those defects resulting from the complete loss of a photopigment type.

Most defects (about 6-8% of the male population) are the result of possessing a photopigment with shifted spectral sensitivity. Individuals who possess a spectrally shifted pigment are known as anomalous trichromats, and their color vision differs from that of normal trichromats in characteristic ways. Anomalous trichromats require a mixture of at most three wavelengths to match any single wavelength in the spectrum, as color-normal observers do. However, in anomalous trichromacy the relative wavelength sensitivity between the cone types is altered and this results in deviations in color matching and often a reduction in color discrimination compared to normals. Protanomalous trichromats have a LWS cone pigment whose spectral sensitivity is shifted toward shorter wavelengths, making protanomalous observers relatively insensitive to longer wavelength lights compared to the normal trichromat. Deuteranomalous trichromats have a MWS cone pigment whose spectral sensitivity is shifted toward the longer wavelengths,

making deuteranomalous observers slightly less sensitive to lights in the middle of the spectrum than the normal trichromat.

About 2% of the male population are dichromats and they require at most 2 lights to match any light in the spectrum. Dichromats behave in color matching tasks as if they lack one of their three normal pigments altogether. Deuteranopes lack the normal MWS cone pigment; protanopes lack the normal LWS. Deuteranopes and protanopes lack color discrimination in the long wavelength half of the visible spectrum, confusing many colors readily discriminated by normal trichromats. Fewer than 1% of the population have tritan defects involving the SWS cone pigment or defects involving more than one cone type.

The exact cause and nature of dichromacy and anomalous trichromacy have been a topic of study for many years. The suggestion that dichromacy results from lacking one of the normal pigments has been debated since it was proposed by Maxwell (1855) and later formally investigated by Konig (as cited in Hsia & Graham, 1965). Loss or "reduction" theories are best called replacement theories since studies of acuity and photopic luminosity in dichromats indicate that they probably have the same number of functional cones as color-normals (Cicerone & Nerger, 1986). A recent study has found evidence that suggests that this replacement involves replacing both pigments and cones, that is, a protanope would have new

MWS cones filled with MWS pigment, not MWS pigment in LWS cones (Cicerone et al., 1987). This has important implications to all post-receptoral neural processing.

Historically, alternatives to a reduction form of dichromacy included two "fusion" theories. These are (a) that two of the pigments reside in the same cones or (b) that each photoreceptor contains the normal photopigment but that their outputs soon converge creating neural fusion (Aitken, 1873; Fick, 1879 as cited in Graham, 1965). Fusion theories persisted in part because of the large individual differences that were often observed among those diagnosed to have the same type of color vision defect.

These differences are well documented. Psychophysical studies of luminosity differences (Alpern & Pugh, 1977; Wald, 1966; Wilmer, 1950), neutral point variability (Farnsworth, 1943; Hecht & Schlaer, 1936), and dichromat confusion lines (Pitt, 1935) have all reported individual differences. Very often these differences are found to be greater among deuteranopes than among protanopes. These differences can also be quite large: neutral points measured in deuteranopes were found to have a range five times larger than those measured in protanopes (Hecht & Schlaer, 1936). Wilmer (1950) distinguished two types of deuteranopia based on the large differences he observed.

Fusion theories are no longer considered as an explanation for dichromacy, largely due to studies using fundus reflection densitometry (e.g., Rushton, 1965). Those findings have confirmed that the loss of a photopigment type accompanies dichromacy. The study of individual differences has continued but with emphasis on possible variations in photopigment spectral sensitivity and possible variations in neural processing.

The Genetics of Missing or Spectrally-Shifted Photopigments in Protan and Deutan Observers

Although dichromacy may rarely be acquired through injury or disease, the most prevalent forms are inherited. Defects of the LWS and MWS pigments are X-linked and inherited recessively, predominantly by males. Only recently has it been possible to isolate the portions of the X-chromosome where the LWS and MWS pigment genes are located, to determine the exact sequence of the nucleotide base pairs on that segment of DNA, and to compare an individual's color matching behavior to his own genotype (Nathans, Thomas, & Hogness, 1986).

It had always been assumed that there were two gene loci on each X-chromosome, one for the LWS photopigment gene, the second for the MWS photopigment gene (Kalmus, 1965). However, when Nathans et al. studied a small sample of color normal, anomalous, and dichromatic males they found that in their sample men had at most one copy of the LWS photopigment gene, but different men could have

more than one copy of the MWS photopiment gene. It was not unusual to find two or three copies of the MWS gene and some people had as many as five. Several showed copies of a gene that was composed of different portions of a LWS gene and a MWS gene. These hybrid genes were sometimes found in place of a normal gene and other times in addition to the expected complement of normal genes.

Comparing gene copy numbers to color matching behavior, it was found that different genotypes could give rise to the same phenotype. Dichromats were missing either the LWS photopigment gene (associated with behavioral protanopia) or the MWS photopigment gene (associated with behavioral deuteranopia). Some dichromats also had hybrid genes in place of these missing genes. These hybrid genes might be responsible for producing pigments with unusual spectral sensitivity. In other cases the hybrid genes appear to be phenotypically silent, having no measurable effect in color matching. At present, not much is known about how these hybrid genes relate to color matching behavior.

Interestingly, in a recent study analyzing the fusion genes of anomalous trichromacy, Neitz et al. (1989) report that there appear to be no differences in the fusion genes found in individuals with color defects of different severity. They believe that since some of the differences among anomalous trichromats are not associated with differences in the photopigment genes they are

probably not due to differences in the spectral sensitivities of the photopigments.

Normal Human Color Vision Relies on Color-Opponent Neural Processing

When stimulated, the individual cones have only a single category of response, and it is related to the number of quanta caught but independent of their wavelengths. Cones cannot, therefore, inherently signal wavelength composition by themselves and a second process is necessary to derive information about color. This second process is the neural processing of color information that takes place first in the retina. In 1862 Ewald Hering proposed an "Opponent-Color Theory" which hypothesized that the eye contained three sets of mutually antagonistic retinal processes that differentially responded to colored lights falling on the retina. Hering believed that there were red/green, blue/yellow, and black/white pairings that responded with inhibition or facilitation depending upon which light of the color-pair was present in the stimulus. There are many retinal ganglion cells with center-surround organized receptive fields with mutually antagonistic properties similar to those Hering proposed (De Monasterio, 1978).

The exact complement of cone inputs to these cells is unknown at this time. Some physiological and psychophysical data suggest that the inputs to the red/green opponent cells are probably the LWS and SWS

cones to the "red" and the MWS cones to the "green" (Cicerone et al., 1987; DeValois, 1973; Wiesel & Hubel, 1966).

This color-opponent processing is necessary for normal color vision. This is evident when it is absent, either due to disease, drug, or when characteristics of the stimulus prevent color-opponent processing. Certain retinal diseases can selectively affect the lateral retinal connections that subserve opponent processing and have a profound affect on color vision (King-Smith & Carden, 1976). Recently, the tuberculosis medication Ethambutol has been shown to selectively and reversibly interfere with red/green opponent processing in humans and goldfish (Spekreijse et al., 1990). In both cases cone function and general vision are thought to be otherwise unaffected.

Color-opponent processing is susceptible to failure when certain characteristics of the stimulus are non-optimal. It is known that stimuli will not be processed in this way if the stimulus is made too small, too brief in duration, or is imaged on the retinal periphery (see King-Smith & Carden, 1976; Thomas & Kuyk, 1989). These three factors help determine whether a light stimulus will be chromatically processed or not in the color-normal eye.

Possible Neural Processing Abnormalities in Protan and Deutan Observers

Changing the temporal or spatial aspects of color stimuli can affect color discrimination, reveal the presence of "new" photopigments, and can show differences between color-normal and color-deficient observers that are not explainable by differences in photopigment spectral sensitivity. Among color-normal observers, stimulus factors (such as size, duration, and retinal location) can be shown to have effects on the neural processing of color. In the color-normal eye though, the size and duration of the stimulus must be drastically altered to affect chromatic processing in the fovea. But profound effects can be seen in color-normal observers when the stimulus is imaged in the retinal periphery.

When a peripheral region of the retina is used to view colored lights, color appearance and color matching are quite different than when the same lights are viewed fovealy. Color-naming, color-discrimination, and color matches all change when the peripheral retina is used, and in all three cases performance becomes poor and appears deuteranopic (Boynton et al., 1964; Uchikawa et al., 1982).

Wooten and Wald (1973) demonstrated that these changes were not due to photopigment spectral sensitivity differences. They studied detection thresholds for color stimuli imaged out to 80 degrees in the periphery and found three normal cone mechanisms, although the stimulus

had to be significantly enlarged to do so. Their results were also consistent with this idea that color-normals behave deutan-like in the far periphery, i.e., the MWS mechanism appeared to weaken.

A similar type of experiment could not be performed on dichromatic observers because they have only one cone mechanism sensitive in the middle to longwavelength end of the visible spectrum. However, shifts in the dichromat neutral point, that region of the spectrum that appears to have no hue to the dichromat, have been reported which suggest an analogous process. These shifts were found to be much larger for deuteranopes than protanopes, and the authors postulated that this was probably due to a relatively larger sensitivity loss in the MWS mechanism than the LWS (Massof & Guth, 1976).

Several studies have investigated temporal factors which affect the color vision of those with color vision defects. A study using flickering stimuli has reported finding that carefully screened dichromats can show the presence of a third anomalous photopigment (Frome, Piantanida, & Kelly, 1982) and other studies using alternating comparison/standard fields have found that the match range of anomalous trichromats can be reduced relative to conditions not using alternation (Nagy et al., 1985; Nagy & Purl, 1987). These studies suggest that post-receptoral processes are involved. Differences in post-receptoral processing between normals and dichromats

were found by Dain and King-Smith (1980). They studied temporal integration in dichromats and normals and found that the total integration time in dichromats was 40% shorter than that in color-normals.

Many studies have also investigated the influences of spatial factors. The early 20th century vision researcher Nagel (as cited in Smith & Pokorny, 1977) did not have normal color vision and in experiments performed on himself noticed that he behaved as a dichromat when tested with a small field but he became an anomalous trichromat when tested with a large field (about 2 deg.). Several studies have shown that many individuals initially diagnosed as dichromats behave as anomalous trichromats when tested with large fields (Breton & Cowan, 1971; Smith & Pokorny, 1977). These kinds of dichromats are not rare: all 17 subjects initially diagnosed to be deuteranopes in one study all behaved as anomalous trichromats when tested with a large field (Nagy, Purl, & Houston, 1985). The pigment which is revealed was once thought to be rhodopsin, the photopigment in the rod photoreceptors, but is now known to be a cone photopigment similar to the anomalous photopigments in anomalous trichromacy. Even what is generally considered rigorous screening for dichromacy (accepting the entire Rayleigh match range, failing the Ishihara Plates, and having a neutral point) does not always detect individuals who will become trichromatic when tested with large stimuli.

Stimulus size also affects anomalous trichromats. Color discrimination in anomalous trichromats can be improved by testing with larger stimuli. Nagy (1982) found that the Rayleigh match ranges of anomals became more narrow in some subjects when tested with 10 deg stimuli.

CHAPTER 2

PURPOSE OF THE PRESENT STUDY

Inherited red/green color vision problems (protan and deutan) involve photopigment deficiencies and they also seem to involve neural ones. Temporal and especially spatial integration factors seem to influence anomalous and dichromatic observers to a much greater degree than color-normals.

When tested with large stimuli many "dichromats" show the presense of third pigments which are similar in spectral sensitivity to the anomalous pigments of anomalous trichromacy. When tested with large stimuli many anomalous trichromats also show significant reductions in the size of their Rayleigh match range (i.e., improved color discrimination).

Principal Hypotheses

Since stimulus size can affect color discrimination among many anomalous trichromats and can make some apparent "dichromats" trichromatic, it seems likely that some individuals with these defects may differ in their ability to integrate color information across large areas of the retina or may differ in the size of the retinal

areas that are effectively color-opponent. Color discrimination is hypothesized to be influenced by color-opponent neural processing. This study investigates this hypothesis by measuring changes in color discrimination as a function of field size and compares them to an independent measure of color-opponent neural processing made at the same field sizes for the same observers.

The hypothesis that color discrimination is influenced by color-opponent processing leads to several predictions concerning observers with color defects of different severities and also to predictions concerning changes with field size. First, observers who have normal color discrimination would be predicted to have normal color-opponent strength, the magnitude of which is dependent on stimulus factors and thus on the implementation of this study. In color-normal observers, color discrimination typically is affected very little by stimulus size and color-opponent strength has been found to be fairly constant for foveated stimuli larger than .3 degree and smaller than 2 deg (Guth et al., 1968). Secondly, dichromatic observers, who have no color-discrimination at any field size, should have no measurable color-opponency at any field size. Thirdly, anomalous trichromats would be predicted to have color-opponent strength correlated with their color discrimination. Anomalous observers with poor color discrimination should resemble dichromats, while those

with good color discrimination should have measurable color-opponent strengths. It follows that large field anomalous trichromats would be predicted to have no color-opponency at field sizes where they behave as dichromats, and to have measurable color-opponency at field sizes where they behave as anomalous trichromats. It may be possible that some anomalous trichomats with color discrimination comparable to that of color-normal observers may have color-opponent strength indices similar to those of color-normal observers.

Previous Work

The most closely related work to the present study was performed by Romeskie in 1978. She studied color discrimination and color-opponent strength in 2 color-normal and 6 anomalous observers. Romeskie used the Rayleigh match as a measure of color discrimination. To measure color-opponent strength she used the hue-cancellation technique of Hurvich and Jameson (1955). In this task a small desaturated amount of red or green light is uniformly added to a white light background and the subject is required to add some amount of its complement to the field to eliminate or cancel any appearance of color.

Romeskie found that reduced color discrimination in anomalous trichromacy was correlated with reduced color opponency: larger Rayleigh match ranges (poorer

discrimination) were associated with requiring larger amounts of the color complement to cancel the apparent color (less color-opponent strength). She also related the hue-cancellation measure of color-opponent strength to the Smith-Pokorny cone fundamentals. She concluded that it was not clear whether the reduced opponency and color discrimination were the result of possessing anomalous pigments (closer in spectral sensitivity than the normal photopigments) or instead due to neural factors.

There are three drawbacks to the Romeskie (1978) study. First, her anomalous observers all had very small match ranges. Only exceptional discriminators would have match ranges of the sizes she reported when viewing her 1 degree stimulus. This type of study has not been performed on extreme anomalous observers who are poor discriminators but are nonetheless trichromatic. Second, Romeskie used only a 1 degree field for both Rayleigh matching and hue cancellation. This type of study has also not been done using more than one field size. Since photopigment spectral sensitivity is not known to change with eccentricity and the effects of self-screening (pigment density) are small, the presence or absence of changes with field size would help answer the question of whether the reduced opponency was a result of pigment shift or spatial integration factors. Third, it is not known whether changes in color opponent strength might accompany the changes in color discrimination that are

observed among some anomalous trichromats when they are tested with different field sizes. This type of study has not been performed on observers who may behave as a dichromat when tested with a 1 degree field such as Romeskie used, but behave as anomalous trichromats at larger field sizes (i.e., "large field trichromats").

Outline of the Present Study

The Farnsworth-Munsell 100-hue test and the Rayleigh match were used to classify all observers and the Rayleigh match range was used as a measure of color discrimination. The latter task is one of the most conventional methods for testing color discrimination in the longwavelength half of the spectrum. The bichromatic mixture threshold technique was used to index color-opponent strength. This technique relies on increment thresholds rather than on color appearance (e.g. hue cancellation method; Hurvich & Jameson, 1955). The rationale for using these methods and previous research is discussed in the following sections.

Classification of Normal, Protan, and Deutan Observers

All observers were classified using the Farnsworth-Munsell 100-Hue test and the Rayleigh match.

Farnsworth-Munsell 100 Hue Test. The Farnsworth-Munsell 100-Hue Test was used to screen potential observers and to give a general classification of type of

color vision defect. This test requires the observer to arrange colored caps in order according to hue. This test has been widely used for over 40 years and its use has generated a large data base with norms for many different populations.

Rayleigh Match. The Rayleigh match is a color mixture task where the observer is required to mix red and green lights in additive color mixture to match a yellow standard. It is the most commonly used measure of color discrimination for lights in the red/green part of the spectrum. Since performance on this task is a reflection of LWS and MWS photopigment function, it is also used to reveal the type and number of long wavelength sensitive photopigments. The ratio of red to green light required for making the Rayleigh match is used to infer the presence or absence of photopigments with normal or anomalous spectral sensitivities.

Dependence of Color Discrimination on Field Size. The effect changing the size of the testing field has on the Rayleigh match range has been studied in dichromats and anomalous trichromats as reviewed in Chapter 1. Recently it was also studied in color-normals. Shevell et al. (1990) varied the size (1-7 degrees) of a Rayleigh match test field and measured changes in match means and ranges. They reported that no significant changes in the size of the match range were found but the match means in most observers shifted a small but significant amount

toward the red as stimulus size was increased. That is, for larger stimuli normal observers required a larger proportion of red light to match the yellow standard than when viewing smaller stimuli.

Bichromatic Mixture Thresholds as a Measure of Color-Opponent Processing

Luminance Additivity

When different lights are combined and presented to the eye there is often luminance additivity; if two lights of equal luminance are added together they often appear to double in effective luminance. This is also true at the detection threshold. Mixing a threshold amount of one light and a thresold amount of a second produces a stimulus of 2X the threshold value. Luminance additivity is known as Abney's Law, and it holds under most circumstances. But Abney's law is known to fail when lights of certain chromaticities are presented to the color-normal eye, particularly when they must be detected against a background light (increment thresholds).

As mentioned previously, the visual system relies in part on inhibitory interactions between cone types to discriminate colors. Activity in color-opponent red/green ganglion cells can be inhibited when their receptive fields are differentially stimulated by longwavelength and mid-wavelength lights simultaneously. In this state these cells require more stimulation (more light) to give the same response than they do in the absense of inhibition.

This inhibition for lights of certain spatial configurations and chromaticities results in sub-additivity in certain tasks.

A comparison of increment thresholds for red or green lights alone with that for red + green (or yellow, the metamer) light can index this inhibition for the red/green opponent system. Thresholds for red light or green light alone are typically about .3 Log units lower than thresholds for yellow lights in the color-normal eye when tested against a white background. In such cases luminance additivity fails by about a factor of two.

Much of the early work on luminance additivity of chromatic lights was done by Guth (Guth, 1967; Guth et al., 1968). He has tested for the presence of inhibitory effects with many combinations of wavelength pairs of lights and observed that the mixture of two lights was less visible than either light presented alone. Some of this work was done using stimuli of different sizes and some with color-defective observers.

Dependence of Mixture Thresholds on Field Size

Guth et al. (1968) tested bichromatic mixture thresholds in color-normal observers at three different field sizes: .33, .66, and 2 degrees of angular subtense. Color-normal observers showed sub-additivity at all three field sizes inasmuch as the bichromatic mixture threshold was elevated relative to the monochromatic thresholds.

They report finding no significant differences in threshold elevation for the three stimulus sizes used. Five dichromats were also tested, but only with the .66 degree field size. All dichromats showed complete luminance additivity, that is, no elevation of the mixture threshold relative to the monochromatic thresholds. Guth et al. did not test their color-normals nor dichromats at larger field sizes, and they did not test any color-anomalous observers.

Important analogous work directed at differences in color-opponent summation areas has been reported by Thomas and Kuyk (1989). Thomas and Kuyk used bichromatic mixture thresholds to investigate changes in color-opponent strength with retinal eccentricity in color normals. They report that the strength of color-opponent processing in normals varied as a function of retinal eccentricity, size and duration of the test flash. They tested at the fovea and 30 degrees in the periphery, used field sizes from 1/2 to 5 degrees, and used 10 and 300 msec stimulus presentations. At the fovea, red/green inhibition could be observed with stimuli as small as 1/2 degree and as brief as 10 msec. At 30 degrees in the retinal periphery however, only the 300 msec, 5 degree field stimuli showed sub-additivity.

The Present Study

In the present study color discrimination, as measured with Rayleigh match ranges, and color-opponent

strength, as indexed with bichromatic mixture thresholds, were compared at several field sizes for observers with different red/green color vision defects. The methods used are presented in the next chapter.

CHAPTER 3

METHODS

Subjects

The subjects in this study were recruited over a period of several months and came from two sources. Seventeen subjects were recruited from the general psychology classes and received course credit for participating. The remaining seven subjects were volunteers who were not compensated in any way. All subjects with color vision deficiencies had been informally tested in the past and were aware they had deficient color vision.

All subjects had normal or corrected to normal visual acuity. Those subjects who required correction wore previously prescribed contact lenses since spectacles could not be worn with the present apparatus.

Two subjects, BAN and CBW, were experienced psychophysical observers who had participated in previous color vision studies in the lab. All subjects (except CBW) were naive to the purposes of the experiment. The type of color vision, number participating, and mean age (with standard deviation) of the subjects are shown in Table 1.

Table 1.

Characteristics of Observers

Color Vision	Number	Age (S.D.)
Normal	6	22 (4.8)
Deutan	11	22 (3.7)
Protan	8	19 (1.3)

Apparatus

Initial Screening: the Fm-100 Hue Test

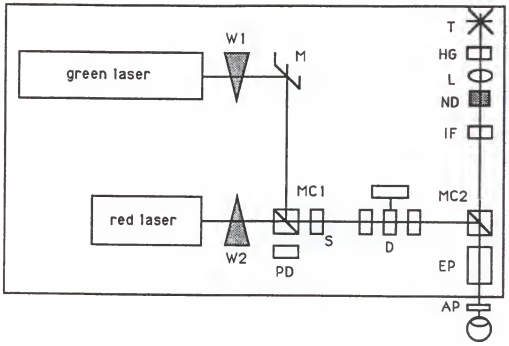
The Farnsworth Munsell-100 Hue test was used to screen potential subjects. The FM-100 Hue Test is comprised of four groups of colored caps manufactured of pigments whose chromaticities lay along different axes of color space. Each of the four boxes must be arranged in order according to hue while being viewed under a special illuminant. The caps were illuminated from a distance of 25 centimeters by a General Electric "Daylight" fluorescent light whose radiant spectrum is comparable to that of light sources recommended for this test. This test is useful for screening because it requires only 20 minutes to complete and is usually successful in diagnosing different color vision defects from characteristic patterns of errors made while arranging the caps.

Instrument for Measuring Rayleigh
Matches and Bichromatic Mixture Thresholds.

A single three channel optical system was constructed for measuring both Rayleigh matches and bichromatic mixture thresholds. A schematic diagram of this system is shown in Figure 1. This system has three light sources: a tungsten lamp (2800K) driven by a regulated 12 volt DC power supply and two low power (.5 mW) Helium-Neon (He-Ne) lasers. The two lasers were tuned by the manufacturers to different lines in the Ne spectrum, one laser (Uniphase Corp.) tuned to the 633nm line and the other laser (Melles-Griot) tuned to the 544nm line. The outputs of these lasers provided monochromatic red and green light, respectively. Light from these sources passed through the optical system as described below.

White light in the tungsten lamp path passed through a condensing lens, heat absorbing glass, and 1.5 Log units of neutral density filter before falling on mixing cube MC2. A circular field stop placed in the image plane at MC2 created a circular field which subtended 12 degrees of visual angle. A variable diameter occluding disk could also be placed here to restrict light in this path to only filling a ring whose outer diameter was always 12 degrees

Figure 1. Instrument used for testing Rayleigh match and bichromatic mixture thresholds. Individual components are listed. See text for details on optical paths.



AP=	Artificial Pupil
D=	Diffusing Glass
EP=	Eyepiece
HG=	Heat Absorbing Glass
IF =	Interference Filter (580nm)
L=	Condensing Lens
M=	Mirror
MC1,2 =	Mixing Cubes
N=	Neutral Filter
PD=	Photodiode
S=	Electronic Shutter
W1,2=	Neutral Density Wedge

but whose inner diameter could be changed. The angular sizes of the occluding disks were .38, .75, 1.5, and 3.0 degrees, and these were the possible inner diameters of the disk/ring stimulus arrangement. A 580nm interference filter could also be placed in this path.

Light from the red and green laser paths passed through separate Inconel 2 Log unit neutral density wedges. A small, thin rod attached to each wedge permitted each path to be occluded when desired. A mirror (M1) in the green laser path allowed both lasers to be optically superimposed at mixing cube MC1. The red and green combined path then passed through an electronic shutter (ES) and passed through a device designed to remove laser speckle. This device consisted of three circular pieces of diffusing glass, equidistant from one another and orthogonal to the light path. The middle diffuser was attached to a mechanical arm which vibrated it at 60Hz. This combination of diffusion and blur from motion eliminated speckle without creating any visible artifacts.

The red and green laser light passed through a variable diameter field stop at MC2. This field stop determined the size of the aperature through which the laser light could pass, and determined the angular size of the central disk. In this study four central field sizes were used in both tasks: .38, .75, 1.5, and 3.0 degrees.

All lights were combined at mixing cube MC2. Light then passed through a focusing eyepiece (Kodak projector lens, 3.5 inch focal length), a 2 millimeter diameter artificial pupil, and then passed through the natural pupil and into the eye.

The different size occluders in the lamp path and the aperatures that were matched in size in the combined red and green laser path created the disk/surround stimulus arrangements used in Rayleigh matching. When no occluder was in place, aperatures created disk/background stimulus arrangements used to obtain increment thresholds. The stimulus arrangements used in both tasks are shown to scale in Figure 2.

In Rayleigh match mode, the 580nm interference filter in the lamp path provided a yellow annulus whose outer diameter subtended 12 degrees. This served as the Rayleigh match standard. The Light from the red and green combined path filled only a variable diameter central disk and provided the comparison stimulus. Separate Inconel neutral density wedges in the red and green paths were rotated in the same direction to change the intensity of the comparison stimulus, or rotated in opposite directions to change its red/green mixture. The yellow standard did not change in wavelength or intensity.

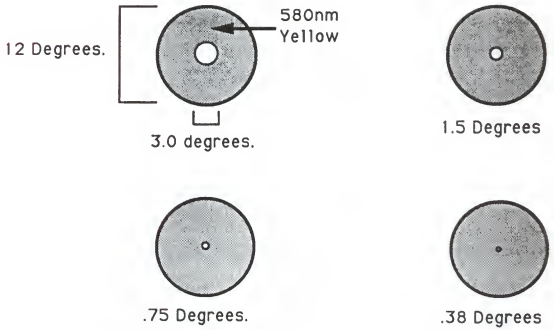
In mixture threshold mode, the 580nm filter and the central disk occluder were removed from the lamp path and

Figure 2. Schematic diagram of the stimulus configurations used in the present study. Drawings are to scale. See text for details.

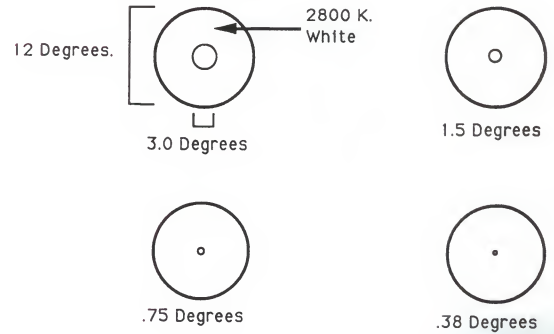
Top: Rayleigh matches.

Bottom: Mixture thresholds.

Rayleigh Match Stimuli



Mixture Threshold Stimuli



it then provided a 12 degree white background field for mixture thresholds. With the occluders removed, light from the red and green laser path produced a light increment disk on this field. The angular size of this increment was determined by the selected size of the apperature in the red and green laser common path. An electronic shutter in the red and green combined path allowed light from one path, the other, both paths, or neither to be presented for a selected amount of time depending upon wedge positions. In this study the test flash duration was always 250msec. Inconel neutral density wedges placed in each path were rotated separately to reduce the intensity of each monochromatic test flash to threshold; rotated together they reduced the mixture red + green to threshold.

The optical system was semi-automated. The Inconel wedges were mounted on stepper-motors (Shinano-Kenshi Corp.) driven by specially written software run on an IBM-AT compatible computer. In full-step mode the wedges could be stepped in 1.8 deg increments, corresponding to .013 of a log unit change (about 1%) in the transmitted light of the Inconel wedges as measured over the log-linear portion of their surfaces (75% of the wedge or 150 steps).

The observer's head was rested on a chin pad and forehead rest that was adjustable along all three axes.

The artificial pupil insured that the subject could be properly aligned with the eyepiece lens.

Light Measurement

The mixing cube MC1 allowed half the red and green light to travel to MC2, pass through the eyepiece and pass into the observer's eye. The remaining light exited mixing cube MC1 orthogonal to the viewed path, passed through a Uniblitz electronic shutter, a photometric filter, and fell on a United Detector Technologies silicon photocell. The voltage generated by the photocell was filtered and amplified by a United Detector Technologies model 40-A Photometer and voltages were read off a Micronta digital voltmeter by the experimenter. This system allowed a direct on-line measure of light intensity in the red, green, or red + green common path.

The relative transmittance of the wedges was measured and calibrated for motor steps using this photocell. For all bichromatic mixture threshold data, a wedge-setting reading was also taken. The luminances in candela/m^2 for the white and yellow backgrounds provided by the tungsten lamp and those in the red and green paths were measured using a Spectra-Pritchard photometer. These measurements were confirmed on another occasion using an SEI photometer.

Procedure

All subjects were first screened with the FM-100 hue test. Each subject viewed and arranged the caps from a viewing distance of approximately 50 centimeters. The caps were illuminated by the "daylight" flourescent source in an otherwise dark room. The cap order in each box was randomized prior to being given to the subject. The order of testing of the four boxes was also randomized across subjects. Subjects were instructed that accuracy was more important than time and that they should take as long as they needed to complete each box. This test was otherwise administered according to the instructions provided in the manual by Farnsworth (1957).

After screening with the FM-100, potential subjects were scheduled for testing with Rayleigh matches and with bichromatic mixture thresholds. Testing sessions were about 1 1/2 hours in length and were held on at least four separate days. On each day the subject made Rayleigh matches and mixture thresholds at a given field size. The order of testing of each field size and the order of the two tasks (Rayleigh matches first or second) were counterbalanced across subjects.

Measuring Color Discrimination with Rayleigh Matches

Task. As outlined previously, the Rayleigh match is a color mixture task where the subject is required to mix

in additive color mixture red and green light primaries in one field to match a yellow standard in another field. The subject is typically required to change the proportion of red and green light and the intensity of the yellow to select a perfect match. In this study, the subject manipulated the red/green mixture and the red/green total intensity to make a match against a fixed intensity yellow standard (580nm, 2.5 log Trolands).

Implementation. All subjects began by sitting in the dark for five minutes and then were asked to view the Rayleigh match stimulus. Each set of matches was always preceded by a practice match, where the subject was introduced to the task and shown how the two types of adjustments (red/green ratio or red/green intensity) altered the appearance of the central circle. The types of settings used by the experimenter and the types of adjustments made by the subjects were not described to them in words (e.g., "this control changes the color"). The subject viewed the Rayleigh match pattern and instructed the experimenter as to the changes needed in the red/green ratio and/or red/green intensity to make his match. Actual adjustments of the stimuli made via the stepper-motors were accomplished through software by commands from the experimenter as instructed by the subject (see below).

The first setting viewed was always a red/green mixture near that of the Rayleigh match of the

experimenter. (It is known from Woods & White (1990) that this experimenter makes a typical normal Rayleigh match; see also Figure 3 below.) The subject was asked to comment on its appearance and then the red/green mixture and/or the red/green intensity adjustments were made to select a match.

Since the types of adjustments were not decribed to them as "color" or "brightness", and since subjects' requests that included a color name were not always reliable, the following procedure was adopted. From initial settings chosen by the experimenter, selected changes in red/green ratio or intensity were made by the experimenter and the subject was asked to report whether the new settings were "better", "worse", or "no different" than the previous ones. When given a reply of "better" the experimenter continued the same adjustment in the same direction changing the red/green ratio or intensity accordingly. With a reply of "worse" the experimenter returned to the previous settings and then started this adjustment in the other direction or switched to the other control (ratio to intensity, or vice versa). If the subject replied "no difference", larger changes were made until the reply was either "better" or "worse".

Subjects were allowed as much time as necessary to find and select a match. All subjects were required to "look away" for 10 or more seconds and then confirm each match before it was accepted. Subjects were encouraged to

make re-adjustments if they were not satisfied. On subsequent matches the experimenter systematically selected red/green ratios more "reddish" and "greenish" as starting points for measuring the extent of the subject's match range.

All color deficient observers were also presented with red alone and green alone to see if they could make a match to the standard using only one primary. At the end of testing, these subjects were also presented with another red/green ratio near that of the experimenter's Rayleigh match, asked to make a match, and questioned as to whether this match was better, worse, or about the same as their previous matches. This procedure was used to ensure that, when measuring the match range, subjects only selected reliable matches.

At least 7 matches were made at each field size, but the first match and the last confirmational match were discarded. The five matches that were recorded were averaged to represent the match mean, while the "reddest" and "greenest" matches were taken to represent the endpoints of the match range. Measurements of the intensity in the red and the green paths were made immediately following each match.

Instructions to the subject. Each subject was instructed that they would be required to make 7 or more color (Rayleigh) matches at each field size. The stimulus was described to them and then they were allowed to view

it while adjusting the chin rest to bring their eye into proper aligment with the artificial pupil. Each subject was cautioned that moving backward from it would cause the outer edge of the stimulus to be "clipped" and to make sure they could always see all of the outer ring (the Rayleigh match standard). Subjects were instructed that they would be required to make the inside circle look identical to the outside ring, such that it was a perfect match not only in color but in brightness. Subjects were encouraged to gaze at various parts of the stimulus as they made adjustments, but to make sure a match was seen when looking directly at the center of the central disk. They were also instructed that they would be required to start from initially random settings of the instrument that were made by the experimenter. Subjects were encouraged to take as much time as necessary to select a match.

Measuring Color-Opponent Strength with Mixture Thresholds

Task. As outlined in Chapter 2, bichromatic mixture thresholds involve measuring 3 separate thresholds for detecting an incremental chromatic test flash (red, green, and red + green) against a white background. The procedures used for finding these thresholds are described below.

Implementation. All bichromatic mixture threshold measures were increment thresholds made against a fixed

intensity tungsten white (2800 K, 3.5 log Trolands) adapting background that subtended 12 degrees of visual angle. Detection thresholds were measured for red (633 nm), green (544nm), and red + green (633nm + 544nm) lights. The duration of these test flashes was always 250msec. The test wavelengths, adapting field, and length of presentation all have been previously shown to maximize detection by red/green chromatic channels while minimizing luminance channel contributions (King-Smith & Cardin, 1976).

Thresholds for the red and green alone and red + green mixture increments presented against the white background were measured using a 2 alternative forced choice procedure (2-AFC) and a staircase adaptive procedure run on 50-trial blocks. The 2-AFC procedure was a temporal forced choice where the inter-stimulus interval was approximately 2 seconds and the inter-trial interval was about 3 seconds. The staircase procedure was a 2down/1up algorithim where two correct responses resulted in a stimulus intensity decrement, one incorrect response response resulting in an intensity increment. A single threshold estimate was derived from each block of trials by computing the average intensity for only those trials after the second reversal (error).

Each subject began by sitting in a dark room for 5 minutes prior to the first series of trials. Before each series of trials, subjects were asked to view the white

background and a 30 second delay followed before the experimenter initiated the first trial. The initial intensity settings for the red and green lights were set on an individual basis such that approximately the first ten trials were usually answered correctly.

Testing for the three thresholds always was performed in the same order: red, green, then red + green mixture. The ratio of red and green light intensities for the red + green mixture stimulus was set to the relative difference in intensity of the two lights at threshold as measured for the red alone and green alone stimuli in that block. This insured that during the red + green trials block the intensity of each light relative to its own threshold was constant. However, this also imposes a testing order in which the red + green mixture threshold is always determined after the red and green monochromatic thresholds have been measured.

Three measures of threshold were made at each field size for the red, green, and mixture stimuli for each subject. After finding the red and green thresholds, both wedges were rotated together to find the red + green threshold.

Light intensities for the red and green increment thresholds were measured immediately following each block of trials. Software computed the average threshold value and sent each wedge to that step value. The experimenter recorded the average step number and recorded the voltage.

The voltage provided an on-line measure that insured the entire system was operating normally, but for the thresholds a 5-point smoothing of the wedge calibration data provided the voltages used in data analysis.

Instructions to the subject. Each subject was told that the purpose of this task was to determine the smallest amount of light that the subject could reliably detect. The 2-alternative forced-choice procedure was explained, and subjects were told that the test flash would always be in one trial interval or the other but never in both nor in neither. Subjects were told that if they were not confident that they saw the flash in either interval that they would need to make a best guess. The staircase adaptive procedure was explained only in that a correct response resulted in a decrement in the intensity of the test flash.

As when performing the Rayleigh match, subjects were cautioned to keep their eye near the artificial pupil to prevent the white background field from becoming "clipped" along its outer edge. Subjects were told that an audible click would signal each interval and be simultaneous with each test flash. These clicks were generated by the electronic shutter which determined the length of stimulus presentation.

Each subject was told that the test flash would appear exactly in the center of the white field. No fixation mark was used, but some fine dust on mixing cube

MC2 was visible and provided points of fixation. The reliable timing of the inter-stimulus and inter-trial intervals obviated the need for a warning stimulus.

Analysis

Farnsworth-Munsell 100-Hue Test

The FM-100 was analyzed in the traditional fashion where color confusion axes were determined by eye from the polar plots of errors. In the event that the FM-100 was inconclusive, an informal Rayleigh match at one of the larger field sizes was used to diagnose the observers type of color vision problem prior to beginning. This information was useful in estimating the wedge settings for the first series of mixture threshold trials.

Color Discrimination

Each subject's color discrimination was categorized according to type and severity of defect, based on the Rayleigh match data. The conventionally used match mean and range of the ratio R/R+G of acceptable matches was used to categorize all subjects. These categories, made at each field size, were (a) normal, (b) simple deuteranomaly, (c) simple protanomaly, (d) extreme deuteranomaly, (e) extreme protanomaly, (f) deuteranopia, and (g) protanopia.

The categorization "Normal" describes those subjects whose match means were comparable to that of the

experimenter, whose Rayleigh match mean and range compared to a large sample of men is shown in Figure 3. It should be noted that the data in this figure were collected on another instrument, and R/R+G is calibrated in radiometric units that will not be directly comparable to data presented later.

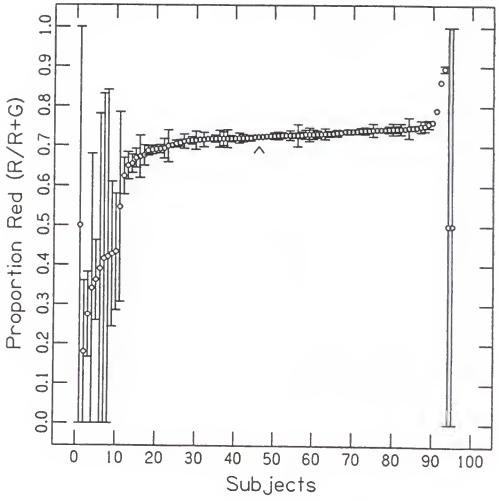
Figure 3 shows the proportion red needed for Rayleigh matches to a 575nm standard by 95 male subjects, from a study by Woods and White (1990). Each point plots the mean of 5 matches and the error bars represent +/- 1 standard deviation for each observer. The data have been sorted in increasing order of the R/R+G ratio of the match mean, except in the cases of three dichromats (leftmost subject = deuteranope, 2 rightmost subjects = protanopes). Data for subject CBW, the present experimenter, are shown above the carat. It is clear that CBW's matches are representative of the normal observers in this large sample.

Both in the present study and that of Woods and White, the simple anomalous observers (protanomalous and deuteranomalous) were those subjects whose match means were different than those of the normal subjects and whose match ranges were smaller than .5 R/R+G units. Extreme anomalous observers were those whose match ranges were larger than .5 R/R+G units, and usually included the normal match range, but did not cover the entire range. Dichromats (protanopes and deuteranopes) were those

Figure 3. The Rayleigh matches of 95 men from a study by Woods and White (1990). The mean +/- 1 std. dev. of the ratio R/R+G are shown. The carat marks data for subject CBW.

NOTE: These data were collected on an instrument calibrated in radiometric units so that the absolute R/R+G values are not directly comparable to those in the present study.

Figure 3


Proportion Red (R/R+G)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
0
10
20
30
40
50
60
70
80
90
100
Subjects

observers whose match ranges covered the entire possible match range. Dichromatic observers matched each primary alone to the standard.

Color-Opponent Inhibition

A measure of additivity of the effects of red and green lights was derived from the mixture threshold data. This was a measure of the magnitude of non-additivity, relative to linear summation, for the red and green thresholds alone compared to the R + G mixture threshold. The measure used for this comparison was the Log Threshold Elevation, which equals

$$\log \left[2 \left(red_{mix} + green_{mix}\right) / \left(red_{mono} + green_{mono}\right)\right]$$

where red_{mix} = red intensity of the bichromatic mixture stimulus at threshold, $green_{mix}$ = green intensity of the mixture stimulus at threshold, red_{mono} = red intensity at monochromatic threshold, and $green_{mono}$ = green intensity at monochromatic threshold.

When there is perfect additivity of the effects of the two lights, the R + G threshold should be equal to the R or the G threshold alone, or, $red_{mix} + green_{mix}$ should be equal to $(1/2\ red_{mono} + 1/2\ green_{mono})$. When this is true, the ratio given above becomes unity. The measure log threshold elevation is in this case equal to zero, and there is no evidence of color-opponent inhibition or any

other non-additive interactions. If the measure log threshold elevation differs significantly from zero then evidence exists of a non-additive interaction involved in the detection of these stimuli. This would be an indication, under the present hypothesis, that the detection of these lights was mediated by color-opponent mechanisms.

Color discrimination, indexed by the range of R/R+G ratios that subjects found to be acceptable color matches, and color-opponent strength, as indexed by the log threshold elevation of the bichromatic mixture, were compared at each field size for individuals within each of the color vision categories above. According to the present hypothesis, smaller match ranges (good color discrimination) should correlate with larger mixture threshold elevations (strong color opponency).

Statistical Comparisons

It was important for the present study to make statistical comparisons among several groups of threshold results for the monochromatic primaries and for bichromatic mixtures. The factors analyzed included color vision diagnosis (color-normal, protan, deutan) and severity of defect (dichromat, extreme anomalous, simple anomalous). These were to be compared against the factors of field size (.38, .75, 1.5, 3.0 degrees) and type of primary (633nm, 544nm). All data, except for those on the

dichromats (n=2), were analyzed with one-way and two-way analyses of variance (ANOVAs) and pair-wise comparisons made with the Tukey Test. These analyses were performed within groups to reveal differences in the factors of field size and color primary type, as well as between groups to reveal significant diagnosis or severity differences for these same factors.

One of the difficulties in statistical analyses of the bichromatic mixture thresholds is their partial dependence upon thresholds for the monochromatic primaries tested alone. Uncertainty in determining the threshold for the 633nm increment, plus the analogous uncertainties in determining threshold for the 544nm increment and for the bichromatic mixture stimulus all contribute variance to measuring the ratio (Log Threshold Elevation) used to index color-opponent strength. Because of this known covariation as well as the small sample sizes it was deemed inappropriate to apply more elaborate multivariate techniques which might be subject to artifactual outcomes.

CHAPTER 4

RESULTS

This chapter is organized such that the differences between individuals with the same types of color vision are discussed first, followed by a discussion of the differences between groups. The within-group differences are emphasized in the next three sections. The FM-100, monochromatic threshold, bichromatic mixture threshold, and Rayleigh match data have been organized according to color vision types for normal (good and poor discriminators), protan (protanope, extreme and simple protanomalous), and deutan (deuteranope, extreme and simple deuteranomalous) observers. Following these sections are the between-group comparisons which analyze (a) changes in bichromatic mixture thresholds and Rayleigh match ranges as a function of field size, and (b) the hypothesized correlation between the index of color discrimination (Rayleigh match range) and that of color-opponent strength (bichromatic mixture threshold elevation). The final section reports an unanticipated trend in the Rayleigh match mean as a function of field size for color-normal observers.

Each of the sections emphasizing within-group differences is organized similarly. First, a table lists the FM-100 Hue test total error scores and color vision type for each observer of the selected group. Second, the results of the monochromatic increment threshold tests are shown as figures for the particular group of observers being considered. Third, each section compares via two-panel figures the observers' Rayleigh match ranges (discrimination index) and mixture threshold elevations (color-opponent strength index), each as a function of field size.

Normal Observers

Farnsworth-Munsell 100 Hue Test

All 6 color-normal observers were administered the FM-100-Hue test following the procedures discussed in Chapter 3. All observers showed error scores and patterns typical of normal observers. This test was, however, found to discriminate among them. The total error scores for each subject are shown in Table 2, while the individual polar plots of errors are shown in the Appendix.

According to the the FM-100 scoring manual by Farnsworth (1957), color-normal observers can be categorized as "average discriminators" if their total error score is between 20 and 100; "superior

discriminators" if it is between 0 and 20; and "low discriminators" if the total number of errors is greater than 100. For the observers in this study, 2 could be categorized as superior, 2 as average, and 2 as low discriminating color-normals. Although the low discriminators had very large error scores they showed no error axes, which ordinarily typify color-deficient observers. The 6 normal observers have been dichotomized into groups with good (CBW, VAL, CLA) versus poor (CJG, RAH, TAG) discrimination. Their Rayleigh match and bichromatic mixture threshold data are discussed separately and presented on separate figures below.

Table 2

FM-100 Hue Test Error Scores for Normal Observers

Subject	Error Score	Farnsworth Class	Present Group
CBW	8	superior	good
VAL	12	superior	good
CLA	40	average	good
CJG	65	average	poor
RAH	192	low	poor
TAG	230	low	poor

Monochromatic Thresholds

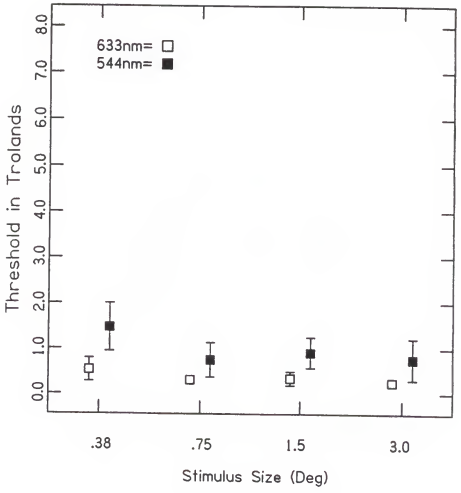
The thresholds for the 544nm and 633nm monochromatic increments on the white background for all color-normal observers are shown in Figure 4. This graph plots mean thresholds in Trolands, a measure of retinal illuminance, for each light (red or green) and each field size (.38, .75, 1.5 and 3.0 degrees). At all field sizes color-normal observers had lower average thresholds for the 633nm light (Average= .35 Trolands) than they did for the 544nm light (Average= .95 Trolands). An analysis of variance (ANOVA) performed on these data found this difference to be significant: $F(1,4)= 28.33$, $p=.006$. This was true at all field sizes (Tukey Test, alpha=.05). Thresholds for 633nm increments did not vary with field size. For 544nm increments, the .38 degree field size had significantly higher thresholds than the other three sizes ($F(3,11)=10.19$, $p=.0017$; Tukey test alpha<.05). The other three field sizes were not significantly different from one another.

Rayleigh Matches: Poor Discriminators

Each observer made 5 recorded Rayleigh matches at each of the 4 field sizes. At each field size, the R/R+G ratios of these five matches was averaged to produce a match mean (used to confirm color vision type) while the "reddest" and "greenest" matches were used to define the

Figure 4. Threshold in Trolands for 544nm and 633nm increments tested at four field sizes for 6 color-normal observers.

Figure 4


633nm= □
544nm= ■
Threshold in Trolands
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
.38
.75
1.5
3.0
Stimulus Size (Deg)

two endpoints of the match range (used to index color discrimination). The match ranges for the three subjects with poor color discrimination are shown in Figure 5A, individual data at each field size displaced laterally for presentation (from left to right: TAG, CJG, RAH). The match ranges can be seen to cover about .10 R/R+G units or less, which is typical of color-normal observers, and are near the color-normal ratio R/R+G for this instrument. The latter was defined by comparison to subject CBW, whose data are shown on the far right at each field size in Figure 6A (below), which shows the data on color-normal good discriminators. The mean R/R+G ratio for subject CBW compared to a large sample of men was shown in Figure 3, Chapter 3, and it confirmed that he is a representative color-normal observer.

Bichromatic Mixture Thresholds: Poor Discriminators

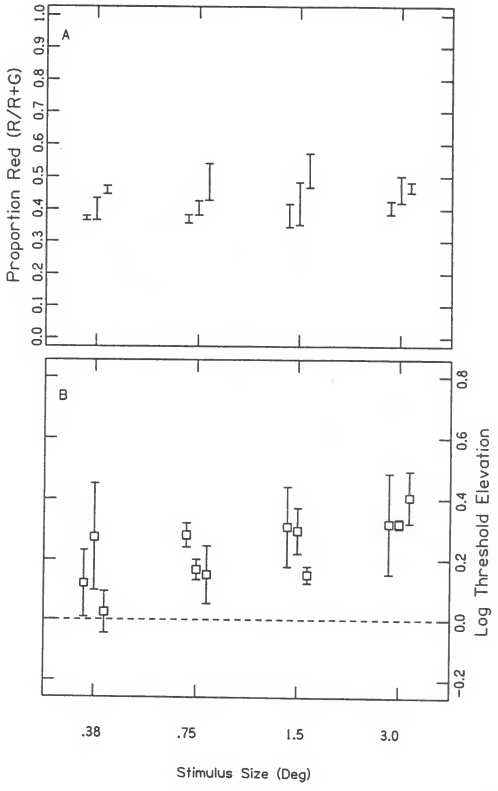
Figure 5B shows the bichromatic mixture thresholds values for the normal observers with poor color discrimination, plotted as a function of field size. At each field size results from observers TAG, CJG, and RAH are shown left to right. These mixture thresholds are given as the Log Threshold Elevations for the 544nm + 633nm mixture stimulus. These were computed by taking the log of the ratio $2(R_{mix} + G_{mix}) / (R_{mono} + G_{mono})$ as described in Chapter 3. Plotted points in Figure 5B show

Figure 5. Rayleigh match ranges and bichromatic mixture threshold elevations as a function of field size for poor discriminating color-normal observers (TAG, CJG, and RAH).

Panel A: Rayleigh match ranges. The vertical lines cover the range from smallest to largest proportion red acceptable for each observer at each field size.

Panel B: Log Threshold Elevation. Mean (+/- 1 std. dev.) of the ratios of bichromatic mixture thresholds to monochromatic thresholds for each observer at each field size. The dashed line represents luminance additivity (Abney's Law).

Figure 5


Proportion Red (R/R+G)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
A
B
Log Threshold Elevation
-0.2
0.0
0.2
0.4
0.6
0.8
.38
.75
1.5
3.0
Stimulus Size (Deg)

means for each observer averaged across replications, while error bars show +/- 1 standard deviation.

The reference line included on Figure 5B (and on several figures below) marks zero Log Threshold Elevation, and it represents Abney's Law of luminance additivity. Deviations of the data from this reference indicate failures of additivity.

The data show a trend of increasing threshold elevations with increasing field size. Mixture thresholds were highest for the 3.0 degree field, the mean Log Threshold Elevation = .373. For the 3.0 degree field, approximately 250% more light was required to bring the mixture 544nm + 633nm to threshold than for the monochromatic lights alone. While the mixture thresholds for poor discriminating normals show around .35 log units of threshold elevation for the 3.0 degree field, they show only about .14 log units elevation for the .38 degree field.

Rayleigh Matches: Good Discriminators

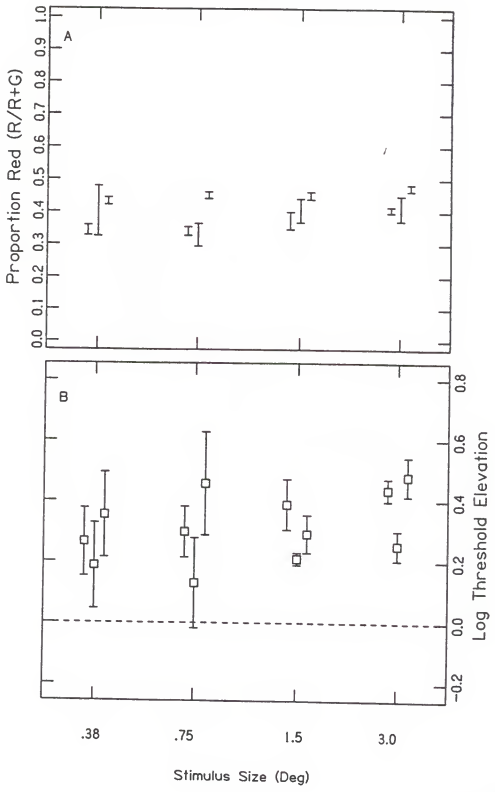
Each of the good discriminating normals also made 5 recorded Rayleigh matches at each of the 4 field sizes using methods in data collection and presentation similar to those for poor discriminating normals presented above. The match ranges for the three subjects with good color discrimination are shown in Figure 6A. At each field size results from VAL, CLA, and CBW are ordered left to right.

Figure 6. Rayleigh match ranges and bichromatic mixture threshold elevations as a function of field size for good discriminating color-normal observers (VAl, CLA, and CBW).

Panel A: Rayleigh match ranges. The vertical lines cover the range from smallest to largest proportion red acceptable for each observer at each field size.

Panel B: Log Threshold Elevation. Mean (+/- 1 std. dev.) of the ratios of bichromatic mixture thresholds to monochromatic thresholds for each observer at each field size. The dashed line represents luminance additivity (Abney's Law).

Figure 6


A
B
Proportion Red (R/R+G)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Log Threshold Elevation
-0.2
0.0
0.2
0.4
0.6
0.8
.38
.75
1.5
3.0
Stimulus Size (Deg)

The two normal subjects with the smallest overall match ranges are shown in this figure.

Bichromatic Mixture Thresholds: Good Discriminators

Figure 6B shows the individual mixture threshold elevations for normal observers with good color discrimination plotted as a function of field size. The format in which the data are plotted in Figure 6B is identical to that of Figure 5B except results are from VAL, CLA, and CBW respectively. The present data show a trend of increasing threshold elevations with increasing field size. While the present data are similar to those of the poor discriminators depicted in Figure 5B, note that the mixture thresholds for good discriminators are larger for the .38 degree field size (.27 log units of elevation) compared to those of poor discriminators (about .14 log unit). Note also that the overlap between the distributions in Figures 5B and 6B is the result of observers CJG (middle observer, Fig. 5B) and CLA (middle observer, Fig 6B). These two observers are the "average" discriminators in Table 2.

ANOVA's performed on the good and poor discriminating normals separately showed no significant changes in Log Threshold Elevation with field size. An ANOVA performed on a data set that included both poor and good discriminating normals showed that the field size differences were statistically significant: $F(3,15)=5.37$,

p=.0104. This finding of significance for the combined data set as opposed to either set alone is probably due to the smaller sample sizes when analyzed separately. Tukey pair-wise comparisons revealed that these differences were only significant between the .38 degree and 3.0 degree fields. An interaction term was significant between group (poor vs. good discriminators) and field size ($F(1,4)=3.62$; $p=.045$), suggesting that the effects of field size are more pronounced for poor than for good discriminators. A F-test for simple effects found no differences between any of the paired comparisons, however.

Protan Observers

Eight protan observers participated in this study. Of these, 1 was found to be a protanope, 3 were extreme protanomalous, and 4 were found to be simple protanomalous as classified by their Rayleigh match ranges. Protanopes make matches that cover the entire match range, extreme protanomalous observers match ranges cover more than .5 R/R+G units but not the entire match range, and simple protanomalous observers match ranges cover less than .5 R/R+G units.

Farnsworth-Munsell 100 Hue Test

The error scores from all 8 protan observers for the FM-100 Hue Test are shown in Table 3.

Table 3

FM-100 Hue Test Error Scores for 8 Protan Observers, Classified From Rayleigh Match Means and Ranges.

	Subject	Error Score
Protanope	CMD	140
Extreme Protanomalous	AAH	49
	EAL	196
	CAS	268
Simple Protanomalous	BAN	12
	MAP	56
	DCF	64
	MWG	347

All subjects could be categorized as protan from the error axis visible in polar plots of their errors except subject BAN who made too few errors to be classified (see the Appendix for the polar plots of all individual data). The classifications in Table 3 of protanope, and extreme

or simple protanomalous were also made on the basis of the Rayleigh matches.

Similar to the FM-100 and Rayleigh match of color-normal observers, a protan observer's FM-100 error score was not particularly predictive of that observers' Rayleigh match range. In each case (except BAN) the error axes accurately predict the category of defect, however.

Monochromatic Thresholds

The thresholds in Trolands for 544nm and 633nm monochromatic increments for all protan subjects, grouped by severity of protan defect, are shown in Figure 7. The three panels in Figure 7 show 544nm and 633nm mean thresholds (+/- 1 standard deviation) for 1 protanope (Panel A), 3 extreme protanomalous (Panel B), and 4 simple protanomalous (Panel C) observers. The thresholds measured for the 544nm increment were similar for all three types of protan observers. However the thresholds for 633nm increments did differ for the three groups. Simple protanomalous observers had lower thresholds than those of extreme protanomalous observers, who in turn had lower thresholds than protanope CMD, for 633nm light.

Protanopes and protanomalous trichromats are relatively less sensitive to lights in the longwavelength end of the spectrum than are normal trichromats. This can be seen by comparing thresholds for the 633nm primary in Figure 7 and Figure 4.

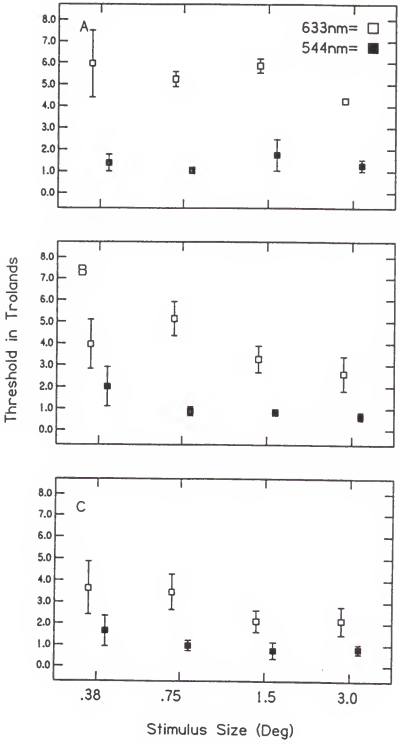
Figure 7. Threshold in Trolands for 544nm and 633nm increments at four field sizes for Protan Observers.

Panel A: Protanope.

Panel B: Extreme Protanomalous.

Panel C: Simple Protanomalous.

Figure 7


A
B
C
633nm= □
544nm= ■
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Threshold in Trolands
.38
.75
1.5
3.0
Stimulus Size (Deg)

Protanope

Rayleigh Matches. The Rayleigh matches for protanope CMD are shown in Figure 8A. Observer CMD could match the 580nm standard using either primary alone, and this fact is represented by the vertical lines that cover the R/R+G range from 0.0 to 1.0. Since this observer can match red alone or green alone to the yellow standard, he is by definition a dichromat, and he was determined to be a protanope from the luminances of each primary alone used in making his matches. Protanopes, lacking the long-wavelength sensitive photopigment, require far more 633nm than 544nm light to match the 580nm standard. Observer CMD behaved as a dichromat at all 4 field sizes.

Bichromatic Mixture Thresholds. The bichromatic mixture thresholds for protanope CMD are shown in Figure 8B. These data are variable but the Log Threshold Elevations are near zero. The data do not appear to change predictably as a function of field size. No statistical analyses were performed on the data from this single observer. However, it is expected on theoretical grounds that Abney's Law should apply to this dichromat and the data are consistent with that expectation.

Extreme Protanomalous

Rayleigh Matches. Figure 9A shows the Rayleigh match ranges for 3 extreme protanomalous observers (left to right at each field size: CAS, AAH, EAL). These

Figure 8. Rayleigh match ranges and bichromatic mixture threshold elevations as a function of field size for protanope CMD.

Panel A: Rayleigh match ranges. The vertical lines cover the range from smallest to largest proportion red acceptable at each field size.

Panel B: Log Threshold Elevation. Mean (+/- 1 std. dev.) of the ratios of bichromatic mixture thresholds to monochromatic thresholds at each field size. The dashed line represents luminance additivity (Abney's Law).

Figure 8

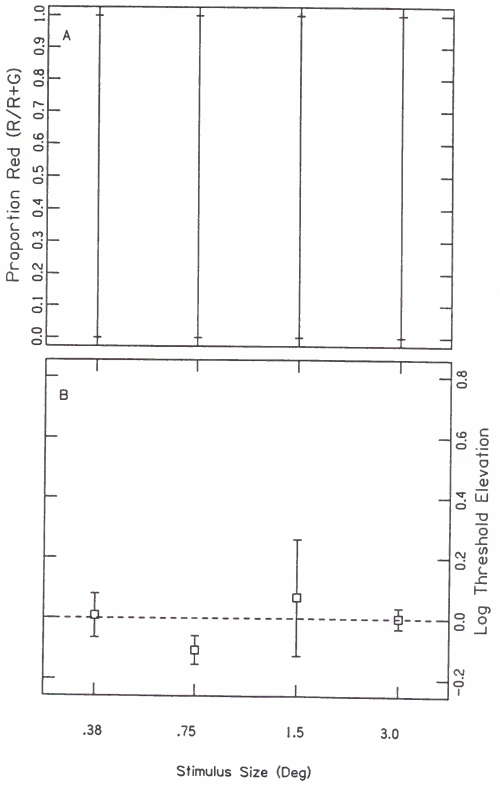
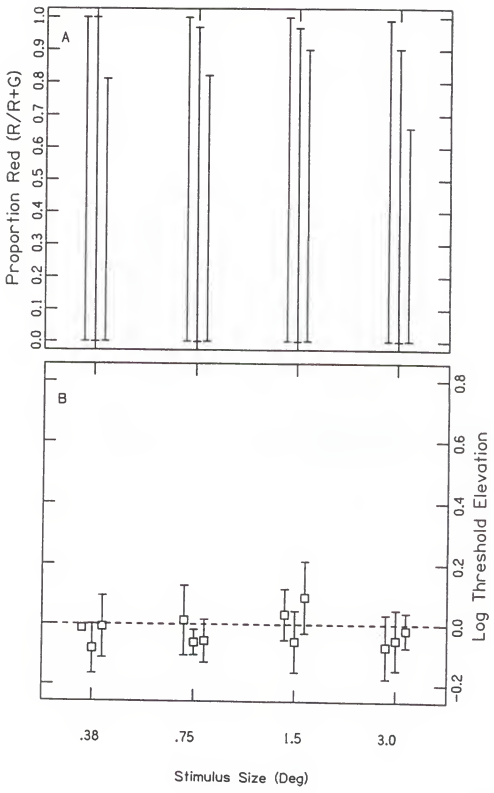

A
B
Proportion Red (R/R+G)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Log Threshold Elevation
-0.2
0.0
0.2
0.4
0.6
0.8
.38
.75
1.5
3.0
Stimulus Size (Deg)

Figure 9. Rayleigh match ranges and bichromatic mixture threshold elevations as a function of field size for extreme protanomalous observers (CAS, AAH, and EAL).

Panel A: Rayleigh match ranges. The vertical lines cover the range from smallest to largest proportion red acceptable for each observer at each field size.

Panel B: Log Threshold Elevation. Mean (+/- 1 std. dev.) of the ratios of bichromatic mixture thresholds to monochromatic thresholds for each observer at each field size. The dashed line represents luminance additivity (Abney's Law).

Figure 9


A
B
Proportion Red (R/R+G)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Log Threshold Elevation
−0.2
0.0
0.2
0.4
0.6
0.8
.38
.75
1.5
3.0
Stimulus Size (Deg)

observers were classified as extreme protanomalous since their Rayleigh match ranges covered more than .5 R/R+G units at all field sizes but not the whole match range when tested with the 3.0 degree field. All three extreme protanomalous observers' Rayleigh match ranges were affected by changes in field size. Observer CAS (leftmost) behaved as a dichromat at .38, .75, and 1.5 degrees but always required about 2% green light in order to make a match at the 3.0 degree field. Observer AAH behaved as a dichromat at the .38 degree field but required varying amounts of the green primary in his match at the other field sizes. By convention, both of these observers would be termed "large-field trichromats". The third and fourth extreme anomalous observers behaved as extreme protanomalous trichromats at all four field sizes.

Bichromatic Mixture Thresholds. Figure 9B shows the bichromatic mixture thresholds for 3 extreme protanomalous observers. These data are very close to zero Log Threshold Elevation, and average approximately -.03 log units. No significant changes were seen across field size: $F(3,6)= .080$, $p=.9671$.

Simple Protanomalous

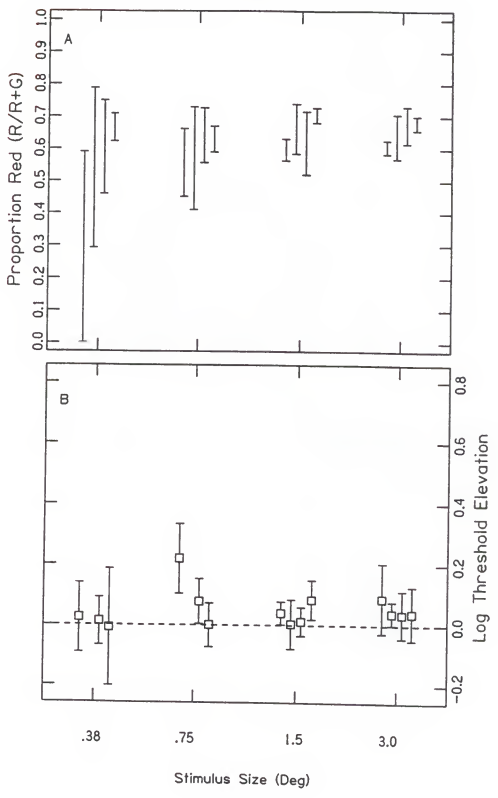
Rayleigh Matches. The Rayleigh match ranges for 4 simple protanomalous observers are shown in Figure 10A (left to right at each field size: MAP, MWG, DCF, BAN). These observers were classified as simple protanomalous

Figure 10. Rayleigh match ranges and bichromatic mixture threshold elevations as a function of field size for simple protanomalous observers (MAP, MWG, DCF, and BAN).

Panel A: Rayleigh match ranges. The vertical lines cover the range from smallest to largest proportion red acceptable for each observer at each field size.

Panel B: Log Threshold Elevation. Mean (+/- 1 std. dev.) of the ratios of bichromatic mixture thresholds to monochromatic thresholds for each observer at each field size. The dashed line represents luminance additivity (Abney's Law).

Figure 10


A
B
Proportion Red (R/R+G)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Log Threshold Elevation
-0.2
0.0
0.2
0.4
0.6
0.8
.38
.75
1.5
3.0
Stimulus Size (Deg)

since their Rayleigh match ranges covered less than .5 R/R+G units when tested with the 3.0 degree field. The Rayleigh match ranges for all 4 observers were affected by changes in the size of the test field and in all cases the Rayleigh match ranges became smaller as the test field size increased. In two cases (observers MAP and MWG) these changes were large and important diagnostically; these observers behaved as extreme protanomalous when tested with the .38 degree field size but behaved as very good discriminating simple protanomalous when tested with the 1.5 and 3.0 degree field sizes. Two of these observers' match ranges at the 1.5 and 3.0 degree fields were roughly comparable in size to the match ranges of poor discriminating normal observers. Their match means were quite different however; approximately .4 R/R+G units "redder" than normals, hence their protanomalous diagnosis.

Bichromatic Mixture Thresholds. Thresholds for the 4 simple protanomalous observers are shown in Figure 10B. Observer MWG made threshold observations only at the 1.5 and 3.0 degree fields. The data for simple protanomalous are, on average, .07 log units higher than those for extreme protanomalous observers. These data also did not vary as a function of field size ($F[3,7]=1.57$, $p=.2807$).

Deutan Observers

Farnsworth-Munsell 100 Hue Test

Table 4

FM-100 Hue Test Error Scores for 11 Deutan Observers, Classified from Rayleigh Match Means and Ranges.

	Subject	Error Score
Deuteranope	WHP	196
Extreme Deuteranomalous	DWW	70
	JTC	160
	JKL	198
	BSB	213
	PAV	275
Simple Deuteranomalous	EAB	115
	JDB	150
	OAA	222
	CAC	268
	HAG	271

The error scores for all 11 deutan observers for the FM-100 Hue Test are shown in Table 4. All subjects could be categorized as deutan from the error axis visible from the polar plot of their errors. The individual polar plots of the errors are shown in the Appendix. The classification in Table 4 of deuteranopia, and extreme or simple deuteranomalous was also made on the basis of the Rayleigh match data.

Similar to color-normal and protan observers, the FM-100 error scores were poor predictors of Rayleigh match ranges but error axes always correctly diagnosed a deutan color vision defect. As a group these deutan observers made more errors on the FM-100 than did protan observers with the analogous severity of defect.

Monochromatic Thresholds

The thresholds for detecting 544nm and 633nm monochromatic increments for deutan observers are plotted in Figure 11. Mean thresholds (+/- 1 standard deviation) are shown for 1 deuteranope (Panel A), 5 extreme deuteranomalous (Panel B), and 5 simple deuteranomalous observers (Panel C). Not all observers made threshold observerations at all field sizes, as outlined below. The increment thresholds for the 633nm light were similar for the three different groups. The thresholds for the 544nm light were also similar for the three groups but did differ significantly from thresholds for the 633nm stimulus for both extreme

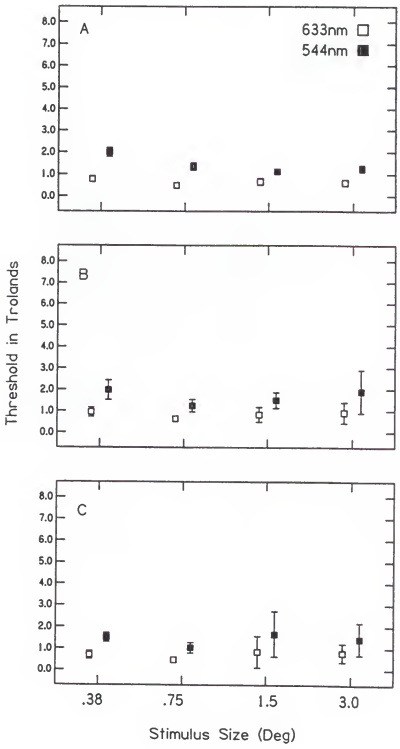
Figure 11. Threshold in Trolands for 544nm and 633nm increments at four field sizes for Deutan observers.

Panel A: Deuteranope.

Panel B: Extreme Deuteranomalous.

Panel C: Simple Deuteranomalous.

Figure 11


A
633nm
544nm
B
C
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Threshold in Trolands
.38
.75
1.5
3.0
Stimulus Size (Deg)

deuteranomalous ($F[1,3]=84.73$, $p=.0027$) and simple deuteranomalous ($F[1,4]=25.00$, $p=.0075$) observers. Like the color-normal but unlike the protan observers, the standard deviations of the 544nm thresholds were larger than those for the 633nm thresholds. As a group, the deutan observers had comparable 633nm thresholds to the group of color-normal observers but their thresholds for 544nm light were, on average, 50% higher than normal.

Deuteranope

Rayleigh Matches. The data from deuteranope WHP are shown in Figure 12A. Observer WHP could match the 580nm standard using either primary alone just as could protanopic observer CMD. WHP is also a dichromat, and he was determined to be a deuteranope from the luminances of each primary alone used in making a match to the 580nm standard. Deuteranopes lack the middle-wavelength sensitive photopigment and require more 544nm than 633nm luminance to match the 580nm standard, while the converse is true for protanopes. Observer WHP behaved as a dichromat at all 4 field sizes.

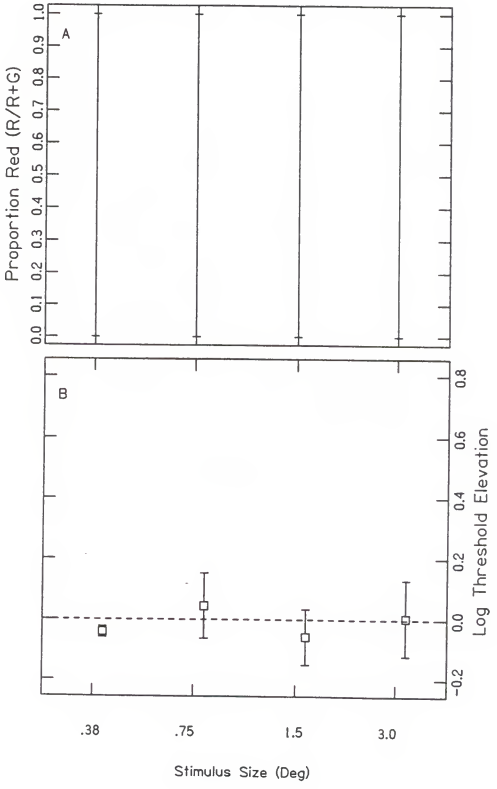
Bichromatic Mixture Thresholds. The bichromatic mixture thresholds for deuteranope WHP are shown in Figure 12B. These data lie near zero Log Threshold Elevation and Abney's Law applies as expected to this dichromat. There do not appear to be any changes in Log Threshold Elevation with field size. As was the case with protanope CMD, no

Figure 12. Rayleigh match ranges and bichromatic mixture threshold elevations as a function of field size for deuteranope WHP.

Panel A: Rayleigh match ranges. The vertical lines cover the range from smallest to largest proportion red acceptable at each field size.

Panel B: Log Threshold Elevation. Mean (+/- 1 std. dev.) of the ratios of bichromatic mixture thresholds to monochromatic thresholds at each field size. The dashed line represents luminance additivity (Abney's Law).

Figure 12


A
Proportion Red (R/R+G)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
B
Log Threshold Elevation
-0.2
0.0
0.2
0.4
0.6
0.8
.38
.75
1.5
3.0
Stimulus Size (Deg)

statistical analyses were performed on the data from this single deuteranopic observer.

Extreme Deuteranomalous

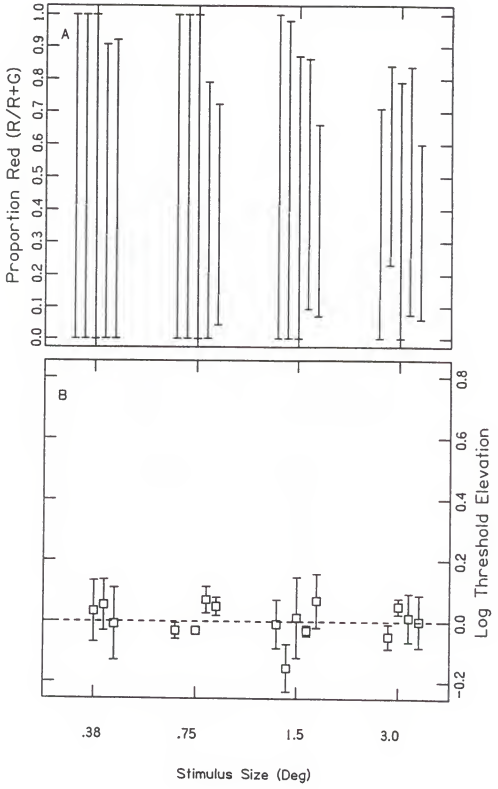
Rayleigh Matches. Figure 13A shows the Rayleigh match ranges for 5 extreme deuteranomalous observers (left to right at each field size: BSB, PAV, JTC, JKL, DWW). These observers were classified as extreme deuteranomalous since their Rayleigh match ranges covered more than .5 R/R+G units at all field sizes, but not the whole match range when tested with the 3.0 degree field. All observers' Rayleigh match ranges were affected by changes in field size. Two of these observers behaved as dichromats at smaller field sizes. Observer BSB behaved as a dichromat at .38, .75, and 1.5 degrees but behaved as an anomalous trichromat when viewing the 3.0 degree field. Observer JTC behaved as a dichromat at .38 and .75 degrees but behaved as an anomalous trichromat at 1.5 and 3.0 degrees. Both of these observers would be termed "large-field trichromats". Observers JKL and DWW behaved as deuteranomalous trichromats at all four field sizes. It was generally true, especially with the 3.0 degree field, that this sample of 5 extreme deuteranomalous observers had better color discrimination than the sample of 3 extreme protanomalous observers.

Figure 13. Rayleigh match ranges and bichromatic mixture threshold elevations as a function of field size for extreme deuteranomalous observers (BSB, PAV, JTC, JKL, and DWW).

Panel A: Rayleigh match ranges. The vertical lines cover the range from smallest to largest proportion red acceptable for each observer at each field size.

Panel B: Log Threshold Elevation. Mean (+/- 1 std. dev.) of the ratios of bichromatic mixture thresholds to monochromatic thresholds for each observer at each field size. The dashed line represents luminance additivity (Abney's Law).

Figure 13


Proportion Red (R/R+G)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
A
B
Log Threshold Elevation
-0.2
0.0
0.2
0.4
0.6
0.8
.38
.75
1.5
3.0
Stimulus Size (Deg)

Bichromatic Mixture Thresholds. Mixture thresholds for 5 extreme deuteranomalous observers are shown in Figure 13B. Observer BSB only made observations at the .75 and 1.5 fields and observer PAV made them only at the 1.5 and 3.0 degree fields. There are individual differences in the Log Threshold Elevations but as a group they average near zero Log Threshold Elevation. Unlike the deuteranope shown in Figure 12, some subjects have mixture thresholds that are above the zero Log Threshold Elevation reference line. There was no significant effect of field size: $F(3,9)=.62$, $p=.6181$.

Simple Deuteranomalous

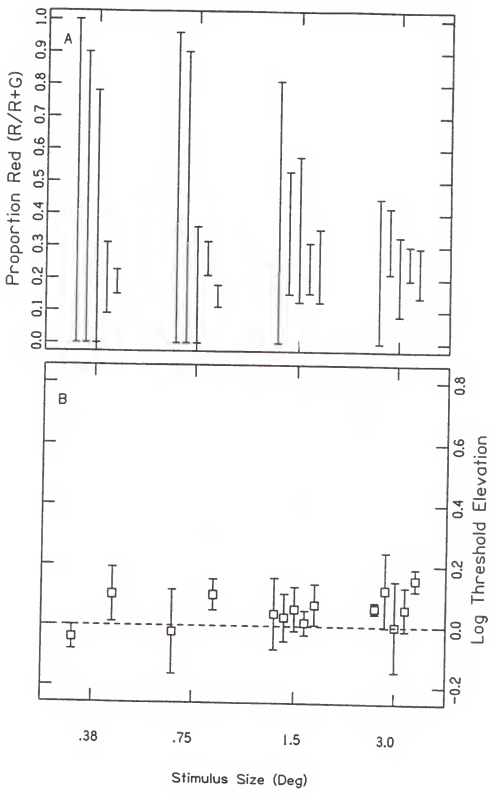
Rayleigh Matches. The Rayleigh match ranges for 5 simple deuteranomalous observers are shown in Figure 14A (left to right at each field size: JDB, HAG, CAC, EKB, OAA). These observers were classified as simple deuteranomalous since their Rayleigh match ranges covered less than .5 R/R+G units when tested with the 3.0 degree field. The Rayleigh match ranges for all observers were affected by changes in the size of the test field and in all cases the Rayleigh match ranges became smaller as the test field was increased in size. In three cases (observers CAC, EKB, and HAG) this change was diagnostically significant; these observers behaved as extreme deuteranomalous trichromats when tested with the .38 degree field size but had good color discrimination

Figure 14. Rayleigh match ranges and bichromatic mixture threshold elevations as a function of field size for simple deuteranomalous observers (JDB, HAG, CAC, EKB, and OAA).

Panel A: Rayleigh match ranges. The vertical lines cover the range from smallest to largest proportion red acceptable for each observer at each field size.

Panel B: Log Threshold Elevation. Mean (+/- 1 std. dev.) of the ratios of bichromatic mixture thresholds to monochromatic thresholds for each observer at each field size. The dashed line represents luminance additivity (Abney's Law).

Figure 14


Proportion Red (R/R+G)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
A
B
Log Threshold Elevation
-0.2
0.0
0.2
0.4
0.6
0.8
.38
.75
1.5
3.0
Stimulus Size (Deg)

(simple deuteranomaly) when tested with the 1.5 and 3.0 degree field sizes.

Bichromatic Mixture Thresholds. Mixture thresholds for the 5 simple deuteranomalous observers are shown in Figure 14B. Subjects EKB, HAG, and CAC only made threshold judgements with the 1.5 and 3.0 degree fields. The data can be seen to be, on average, about .05 units of Log Threshold Elevation. There was no significant increase in Log Threshold Elevation with changes in field size; $F(3,6)=.47$, $p=.7122$.

Match Range and Mixture Threshold Comparisons Between Groups

Match Range

Comparisons of the Rayleigh match range were made between groups using ANOVA's. The F-values and associated probabilities for the tests performed are shown in Table 6. These verify the categorization of observers into normal, extreme, and simple types as based on the diagnostic conventions discussed above. When tested by ANOVA, the comparisons normal vs. simple, simple vs. extreme, and those comparisons of different severities for the same defect (extreme vs. simple protan, extreme vs. simple deutan) all showed significant differences in the Rayleigh match range. Those comparisons for the same severity, different defect (extreme protan vs. extreme

deutan, simple protan vs. simple deutan) showed no significant differences in the size of the Rayleigh match range.

Table 6.

F-values and Probabilities for ANOVA's Comparing Normal, Extreme and Simple Anomalous Rayleigh Match Ranges.

Comparison	F-value	Prob.
Normal vs. Simple	7.01	.0201
Simple vs. Extreme	34.32	.0001
Extreme vs. Simple Protan	95.61	.0002
Extreme vs. Simple Deutan	9.22	.0162
Extreme Protan vs. Extreme Deutan	0.90	.3784
Simple Protan vs. Simple Deutan	2.40	.1653

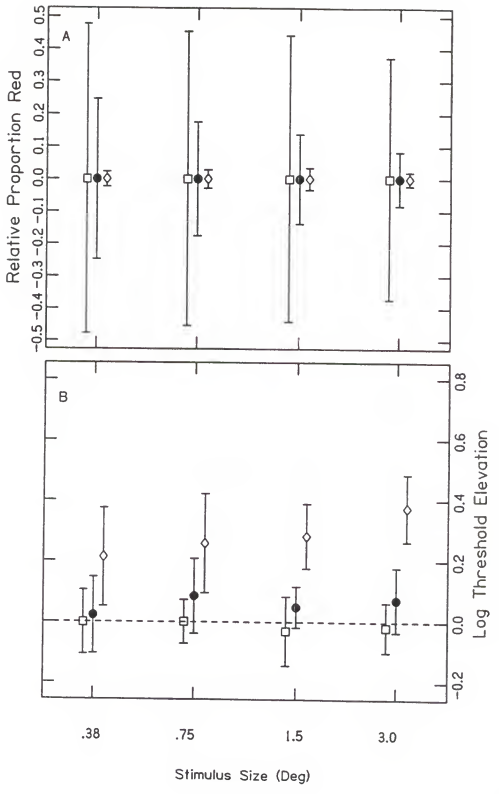
Since there were no differences in the size of the Rayliegh match range for extreme protan vs. deutan, and between simple protan vs. simple deutan, these data were combined to arrive at an average Rayleigh match range for extreme or simple anomalous. The Rayleigh match ranges for normal observers were also averaged, and the averaged match ranges for all extreme, simple, and color-normal observers are shown in Figure 15A. In order to plot these averaged match ranges, the match midpoint of each range for each group of observers has been centered arbitrarily

Figure 15. Relative Rayleigh match ranges and bichromatic mixture threshold elevations shown as group averages for extreme and simple anomalous and for normal observers.

Panel A: Rayleigh match ranges averaged relative to an assigned midpoint of zero R/R+G.
Extreme anomalous (squares)
Simple anomalous (filled circles)
Normal (diamonds)

Panel B: Log Threshold Elevation averages.
Extreme anomalous (squares)
Simple anomalous (filled circles)
Normal (diamonds)

Figure 15


A
B
Relative Proportion Red
−0.5 −0.4 −0.3 −0.2 −0.1 0.0 0.1 0.2 0.3 0.4 0.5
Log Threshold Elevation
−0.2 0.0 0.2 0.4 0.6 0.8
.38
.75
1.5
3.0
Stimulus Size (Deg)

at zero relative R/R+G units. The match ranges are expressed in relative units. Each group of observers is represented by a different symbol.

Mixture Threshold

Comparisons between groups for elevation of the mixture thresholds were also made using ANOVA's. The same comparisons were made for the mixture thresholds as were made for the match ranges, and the F-values and probabilities associated with these tests are shown in Table 7.

Table 7.

F-values and Probabilities for ANOVA's Comparing Normal, Simple and Extreme Anomalous Bichromatic Mixture Thresholds.

Comparison	F-value	Prob.
Normal vs. Simple	34.94	.0001
Simple vs. Extreme	7.48	.0161
Extreme vs. Simple Protan	16.26	.0100
Extreme vs. Simple Deutan	1.49	.2619
Extreme Protan vs. Extreme Deutan	1.80	.2379
Simple Protan vs. Simple Deutan	.130	.7286

Similar to the analyses performed on match range above, the comparisons based on severity (normal, simple,

extreme) of defect showed significant differences. The mean Log Threshold Elevation for normal observers was significantly larger than those means for all other groups. The F-value and probability for this comparison between all normals and all simple anomalous observers is shown in Table 7.

The extreme vs. simple protan comparison was significant while the differences between extreme vs. simple deutan were not. This may be due to larger individual differences among the simple and extreme deutan observers, although statistical comparisons found no significant differences in their means.

The simple anomalous and also the extreme anomalous observers were not significantly different by defect type, so these data were respectively combined. The average Log Threshold Elevations for simple anomalous trichromats were significantly larger than those for extreme anomalous trichromats. Pair-wise comparisons (Tukey Test) revealed that these differences were significant for the 3.0 and 1.5 degree field sizes only; simple and extreme observers had similar thresholds for the .38 and .75 degree fields.

The averaged normal, simple, and extreme anomalous mixture thresholds are shown in Figure 15B as a function of field size. The symbol designation in Panel B corresponds to that in Panel A, so the average Log Threshold Elevation can be compared to the average Rayleigh match range for each group of observers.

Correlation of Match Range and Mixture Threshold

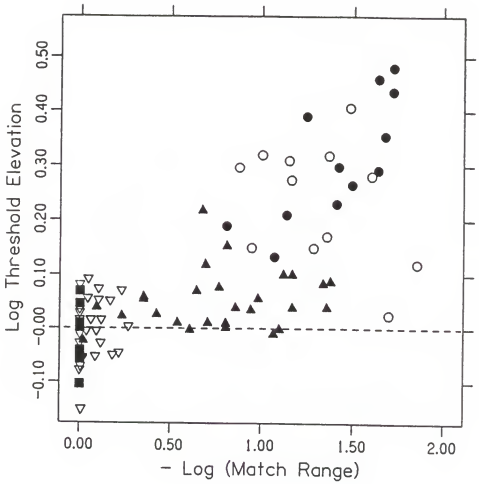
One of the hypotheses of the present study has been that color discrimination (indexed by the Rayleigh match range) is correlated with color-opponent strength (indexed by elevation of the bichromatic mixture threshold). A new type of graph shows all the data on Rayleigh match ranges and mixture thresholds in a single scatter plot. In Figure 16, for each observer the index of color discrimination (-log (Rayleigh match range)) is plotted against the index of color-opponent strength (average Log Threshold Elevation) without regard to field size. Different symbols represent dichromats, extreme anomalous, simple anomalous, poor discriminating, and good discriminating color-normal observers.

On this scatter plot the data fall close to the diagonal from the lower left to the upper right corner. Data in this region represent an inverse relationship between the size of the match range and color-opponent strength. The correlation between the two measures was high ($r^2 = .55$; 86 d.f.; $p < .001$).

On this plot the data for good discriminating normal observers (filled circles) fall mostly in the upper right quadrant; data for dichromats (filled squares) in the very lower left; and data for the extreme (inverted triangles) or simple (filled triangles) anomalous and poor

Figure 16. Log Threshold Elevation as a function of color discrimination index (- log(match range)). Different symbols represent good discriminating color-normals (filled circles), poor discriminating color-normals (open circles), simple anomalous (filled triangles), extreme anomalous (open triangles), and dichromats (filled squares).

Figure 16


Log Threshold Elevation
0.50
0.40
0.30
0.20
0.10
-0.00
-0.10
0.00
0.50
1.00
1.50
2.00
- Log (Match Range)

discriminating normals (open circles) fall between. There is much overlap between the good vs. poor normal observers, but the poor discriminating normals tend show a lower discrimination index and smaller color-opponent strength. The simple anomalous fall in a region between the poor discriminating normals and the zero Log Threshold Elevation reference line, generally with lower discrimination. The extreme anomalous data cluster near the dichromats and near zero for both Log Threshold Elevation and - log (match range).

Several aspects of this plot are noteworthy. First, the data appear to be bounded by the line representing Abney's Law (zero Log Threshold Elevation). Both dichromats and extreme anomalous seem to be adequately described by luminance additivity within experimental error of measurement. Data from normals or simple anomalous do not ever fall significantly below this line. Secondly, a line fit to the normal and simple anomalous data would not intersect the plot at its origin, which is where data for extreme anomalous and dichromats are found. It would instead intersect at about - log(match range) = .19, which is approximately a match range of .72 R/R+G units (r^2 = .40, 50 d.f.; $p < .001$). This may suggest that the dichotomy of simple vs. extreme anomaly that is based on match range size may also reflect a dichotomy in luminance additivity processes. Thirdly, data are absent from the region representing large threshold elevations

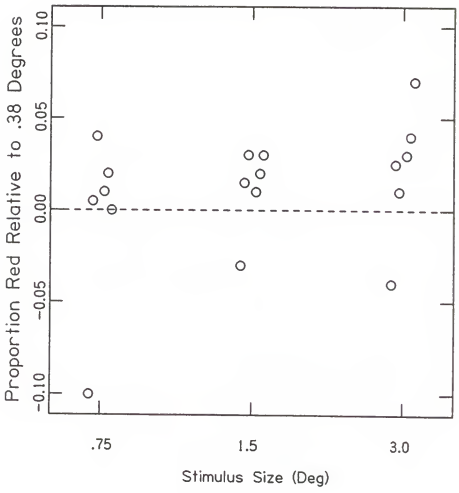
(strong color-opponency) with large match ranges (poor discrimination) and, with the exception of two points, this is also true of the region representing small elevations (weak color-opponency) with small match ranges (good discrimination). The two data points which have the poorest fit to the distribution represent the two normal observers with poorest color discrimination, for the .38 degree field.

Trend of Rayleigh Match Mean with Increasing Field Size for Normal Observers

Figures 5A and 6A above showed that there were no systematic changes in the Rayleigh match range with field size for any of the color-normal observers. The Rayleigh match means did appear to change with field size, however. These data were normalized to account for individual differences as follows. For each subject, the mean R/R+G at the .38 degree field size was arbitrarily set equal to zero and then subtracted from the mean R/R+G values for the .75, 1.5, and 3.0 degree fields. These differences in Rayleigh match means for the three largest fields are shown in Figure 17 using an expanded scale for Proportion Red. For 5 out of 6 observers the mean R/R+G for the .75, 1.5, and 3.0 fields are larger than the respective .38 degree field R/R+G mean. The matches at larger field sizes tended toward slightly larger proportions of the red primary than matches made at the .38 degree field size.

Figure 17. Relative Rayleigh match means as a function of field size for all normal observers. Each mean is plotted relative to each observers match mean for the .38 degree field.

Figure 17


Proportion Red Relative to .38 Degrees
0.10
0.05
0.00
-0.05
-0.10
.75
1.5
3.0
Stimulus Size (Deg)

The present trend appears to support the findings of Shevell et al. (1990), which were reported while the present study was in progress.

CHAPTER 5

SUMMARY AND CONCLUSIONS

Protan and deutan forms of dichromacy and anomalous trichromacy are relatively common color vision defects that have been studied for over a century. The basic genetic mechanisms that give rise to these defects, and the different photopigment combinations that underlie them, are now becoming understood at the molecular level. There remains enough unexplained behavioral heterogeneity among observers who appear to have similar types of defects, though, to indicate that our understanding of these color vision types is not yet complete.

Differences among observers who otherwise seem to possess the same type of color defect include the changes in color discrimination that accompany changes in the size of the color stimulus. Some observers behave very differently when tested with small vs. large stimuli while others do not. Since the spectral sensitivity of the photopigments would not be expected to change under these conditions, except for the possible subtle changes due to self-screening, other factors must be involved. This study examined how color opponent neural processing might

be related to these changes in color discrimination as a function of field size.

The present study investigated an individuals ability to discriminate colors in the longwavelength half of the visible spectrum as well as a measure of color-opponent strength for lights from this same spectral region. Twenty-five observers made Rayleigh matches and bichromatic mixture thresholds at different field sizes to test certain hypotheses about the relationship between discrimination and opponent strength. Of the observers that participated in this study, 6 were color-normal trichromats, 2 were dichromats, and 17 were anomalous trichromats who differed in the type and severity of their deficiencies. All of these subjects were tested with center/surround configured stimuli where the size of the inner disk was varied from .38 to 3.0 degrees. This resulted in small to large continuously viewed comparison stimuli when testing the Rayleigh match, and small to large incremental test flashes when testing the bichromatic mixture threshold.

Summary

Color-Normals

As anticipated, the color-normal observers had the best color discrimination and the largest measured color-opponent strength of any group. For the normal

observers, Rayleigh match range did not change reliably as a function of field size (Figs. 5A, 6A). It may be hard to resolve such changes however, since the very small match ranges of the normals at some field sizes probably approached the measurement error of the system and possibly the error inherent in the psychophysical method (a modified method of adjustment). In other words, there may have been a "floor effect" due to limited resolution. The normal observers whose FM-100 hue test performance was in the range of poor discrimination made Rayleigh matches within ranges that were on average larger but not reliably different from those of the other normal observers.

Color-opponent strength did increase with the size of the testing field (Figs. 5B, 6B). The log threshold elevation of the bichromatic mixture varied from .2 log units for the .38 degree increments up to .32 log units for the 3.0 degree increments. The difference in magnitude between the smallest and largest fields was statistically significant for the group including all color-normals. Poor discriminators on the FM-100 hue test had mixture thresholds that were lower than those of the good discriminating observers at every field size. Also, there was a significant interaction showing that good vs. poor discriminators on the FM-100 seemed to exhibit different rates of change in mixture threshold elevation as a function of field size.

Figure 16 plots the correlation between color discrimination (- log(match range)) and color-opponent strength (Log Threshold Elevation) for all observers. The correlation between the measures accounts for 55% of the variance across groups. There is a substantial amount of overlap in the results from good vs. poor color-normal discriminators according to the FM-100 test, except for two data points obtained with the smallest field size from the two lowest discriminators on the Fm-100 (observers TAG, RAH). These data indicate very low opponent strength with very good color discrimination.

The nature of poor discrimination among normal observers is not well understood. Farnsworth studied it with the FM-100 hue test and found that: (a) it could not be explained by inattentiveness, (b) nor the time taken to complete arranging the caps, and (c) it was very replicable within observers (Farnsworth, 1943). The results of the present study, while based on a small sample of observations may suggest a possible basis contributing to poorer color discrimination among observers who possess the same photopigments; namely, a particularly strong dependence on field size of their color-opponent processes.

Dichromats

The two dichromats that participated in this study showed no ability to discriminate any of the lights in the

longwavelength half of the visible spectrum. Presumably they are missing one of their two middle to longwavelength sensitive photopigments. In one case (protanope) this was the LWS photopigment, and in the second case (deuteranope) it was the MWS photopigment. Given that the dichromats only possessed one photopigment in the longwavelength half of the visible spectrum, and that they could not discriminate colors in that region, it follows that they should show no red/green color opponency. These observers were tested to confirm this expectation and to provide a comparison group for the anomalous trichromats. Athough the sample is small, the two dichromatic observers who participated in this study appeared to show linear summation of the bichromatic mixture threshold relative to their monochromatic thresholds (following Abney's law). The dichromats' performances indicated that their color discrimination did not improve and there was no evidence of color-opponent strength at any of the four field sizes, as expected.

Anomalous Trichromats

The extreme anomalous trichromats (whether protan, Fig. 8A, or deutan, Fig. 9A) all had Rayleigh match ranges larger than .5 R/R+G units, or greater than half the possible range. Typically they could also match the 544nm primary alone to the 580nm standard but never the 633nm primary alone. As a group though, the extreme anomalous

trichromats appeared to show linear summation on the bichromatic mixture threshold task (Figs. 8B and 9B). In fact, their performances were not easily distinguished from those of the two dichromats on this measure. As a group, they had slightly larger color-opponent strength, although whether this amount was statistically significant was not tested (only 2 dichromats in the sample). Figure 16 shows this close similarity in the results from extreme anomalous and dichromatic observers, inasmuch as their respective plotted points show nearly identical distributions near the graph's origin. If the extreme anomalous trichomats have a small amount of color-opponency, then to reveal it would require a much larger sample size of observers and many more observations per subject than used in the present study.

The simple anomalous trichromats had Rayleigh match ranges that were smaller than .5 R/R+G units (Figs 10A and 14A). As a group they showed only a modest amount of color-opponent strength (Figs. 10B and 14B), yet this was significantly more than that of the extreme anomalous observers while significantly less than normals. The simple anomalous trichromats had Rayleigh match ranges that were, on average, about four times larger than the average for color-normals, when tested with the 3.0 degree field. It is interesting to note that the average log mixture threshold elevation is roughly one-fourth that of the color normals (see also Fig.16).

The extreme anomalous trichromats (with poor color discrimination) were associated with unmeasurable color-opponent strength, while simple anomalous trichromats (with better color discrimination) were associated with larger color-opponent strength. For the simple anomalous the mixture threshold elevations were greatest for the 3.0 degree field, although still a factor of four smaller than those of color-normal observers. Interestingly, this was true even for simple anomalous observers whose color discrimination was nearly as good as that of the poor discriminating color-normal observers at some field sizes (there were 4 such individuals).

It was true that the simple protanomalous observers had larger color-opponent strength than the extreme protans but the ANOVA comparison of the simple and extreme deutans failed to reach significance. There may be two explanations for why this was true, and they both involve the particular samples of observers in this study. First, the within-group differences in color discrimination for the simple deuteranomalous observers was large relative to those of the simple protanomalous ones. Second, the color discrimination of the extreme deuteranomalous observers was somewhat better than that of the extreme protanomalous ones. While statistical analyses of the differences between these groups did not indicate significant differences, the deutans, as a group, had more within

group variability and the means for simple and extreme deutan observers were closer together.

Changes With Field Size

Color discrimination was a function of field size for all extreme and simple anomalous observers but not for dichromats. However, there was insufficient evidence to conclude that field size affected color-opponent strength within groups, although several observer's individual data appeared to support this supposition (see subjects JDB and OAA, Fig. 14; BAN, Fig. 10). There were, however, many observers in each group who were unaffected by changes in field size.

Two possibilities suggested themselves as reasons why an effect of field size was not supported by ANOVAs. One possibility is that a small effect of field size was being masked by averaging a subset of subjects, whose color discrimination and color-opponent strength changed measurably with field size, with another subset of observers whose color discrimination and color-opponent strength changed little with field size. To address this, the simple anomalous observers were re-combined into two new groups: simple anomalous observers who had match ranges < .5 R/R+G units at every field size, and those simple anomalous whose match ranges were > .5 R/R+G units (extreme anomalous or dichromatic) at the small field sizes but < .5 R/R+G at the large field sizes. When re-

analyzed in this way, the means differ in the expected direction although the differences are too small to reach statistical significance with the reduced sample size. A second possibility why ANOVA's fail to reveal an effect of field size is that the small number of observers per group and limited number of observations per observer may have prevented small changes from being revealed.

Conclusions

Previous studies have shown that it is possible to eliminate color-opponent processing in color-normals by changing certain characteristics of the stimulus. When this change is a reduction of the size of the stimulus, typically the change must be extreme. For example, a field must be reduced to about .02 degrees before color naming becomes unreliable (Krauskopf, 1964), nearly twenty times smaller than the smallest field used in the present study. Although it may require a much smaller field to eliminate opponency in color-normal observers, the present study shows that it is possible to measure size-dependent declines in color-opponent strength using a procedure that begins with large stimuli and progressively reduces their size in moderate steps.

Unexpectedly, color-normal poor discriminators on the FM-100 hue test appear to show rapid declines in color-opponent strength as field size is so reduced. Although the sample size is small, the significant ANOVA

interaction term (see normal observers, Chap. 4) and the discrepant data points in Figure 16 are consistent with the idea that poor color-normal discrimination may be related to color-opponent processing differences that are size-sensitive.

Color discrimination was found to differ among protan and deutan subjects because it defined the severity of their defects. Both extreme and simple anomalous trichromats' color discrimination was affected by changes in field size as has been reported elsewhere in the literature (e.g., Smith & Pokorny, 1977; Nagy, 1982). For several observers their diagnosis was dependent on field size. Some observers were dichromatic at smaller field sizes but extreme anomalous at larger ones; others were extreme at smaller fields but simple anomalous when tested with larger ones. One observer was dichromatic at the smallest field sizes, extreme anomalous at a middle size, and simple anomalous when tested with the 3.0 degree field.

Romeskie (1978) reported that simple anomalous trichomats had less color-opponent strength than color-normals. Her research has been confirmed and also extended to extreme anomalous and "large-field trichromat" observers by the present study. Normal observers were found to have more color-opponent strength than simple anomalous observers, who in turn had more color-opponent strength than extreme anomalous ones. It was hypothesized

that improved color-discrimination (that often accompanies increases in field size) would be correlated with increases in color-opponent strength. This correlation is emphasized by Figure 16, which shows the expected trend across groups. There was not sufficient evidence to show that the trend of increases in opponent strength with field size was statistically significant by ANOVA's within groups, however, due to individual differences within the groups and small sample sizes.

Future Directions

Several aspects of the present study suggest themselves as areas for future research. This study only investigated one of the many stimulus characteristics which are known to affect normal color-opponent processing, and it has revealed potentially interesting differences between normal and anomalous color vision. How other stimulus characteristics such as temporal factors and retinal location affect color discrimination and color-opponent strength may prove to be important in understanding color-processing in the anomalous eye, and possibly even the poor discriminating color-normal eye.

The differences between extreme and simple anomalous trichomats on the dicrimination/opponent strength correlation were noteworthy. There were differences between these groups that measures of color-opponent

strength or color discrimination alone do not seem to capture.

The present study had no a priori intention of studying differences between poor and good discriminating color-normals, however these data turned out to be quite interesting. Two normal observers were identified who had poorer color discrimination than typical but who had, presumably, the same photopigments since their Rayleigh matches means overlapped those of other normals. However, these individual's color discrimination was poorer and they showed weaker color-opponency than the other normals. This difference was particularly large at the smallest field size. As mentioned above, poor color discrimination among normal observers is not well understood, and the present study could indicate one profitable approach to finding a theoretical basis for these differences.

Lastly, all of the observers in the present study have contributed samples of their DNA in support of a parallel study directed at the molecular genetics of their individual differences. The present study points toward potential differentiations of color vision types which, if validated with larger samples of observers, may help clarify the correlations of color vision genotypes with individual phenotypes.

APPENDIX

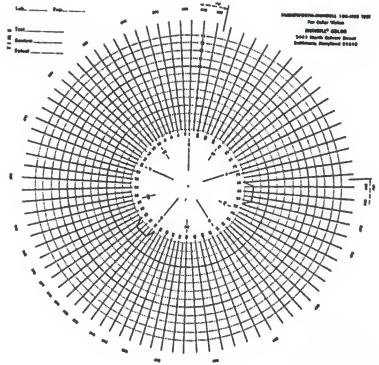
INDIVIDUAL FM-100 HUE POLAR PLOTS

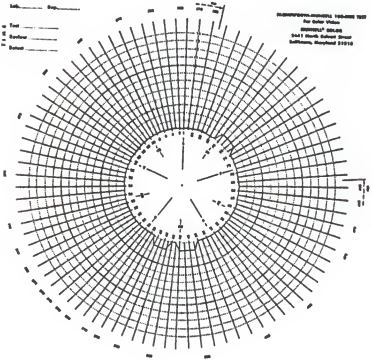
The following pages show photocopies of all individual Fm-100 Hue test polar plots. Table 8 indicates the page each observer's plot is shown.

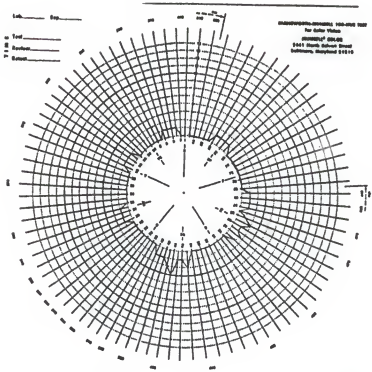
Table 8

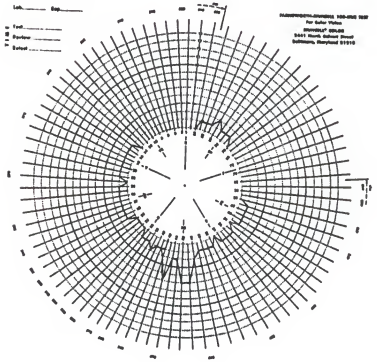
Color vision and page number of FM-100 polar plots for each observer.

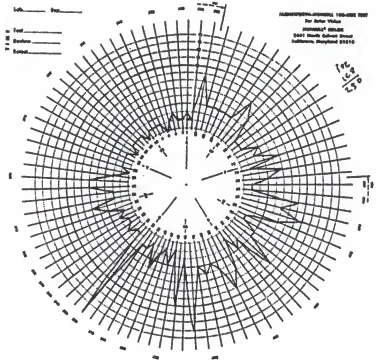
DEFECT	PAGE	SUBJECTS
COLOR-NORMAL	120	CBW, VAL
	121	CLA, CJG
	122	TAG, RAH
PROTANOPE	123	CMD
EXTREME PROTAN	123	CAS
	124	AAH, EAL
SIMPLE PROTAN	125	MAP, MWG
	126	DCF, BAN
DEUTERANOPE	127	WHP
EXTREME DEUTAN	127	BSB
	128	JTC, JKL
	129	PAV, DWW
SIMPLE DEUTAN	130	JDB, HAG
	131	CAC, EKB
	132	OAA

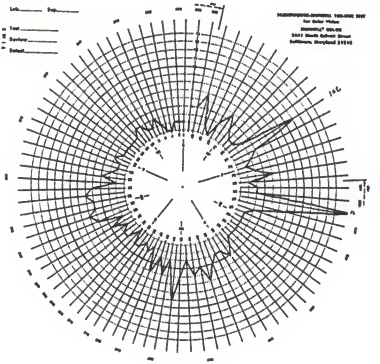


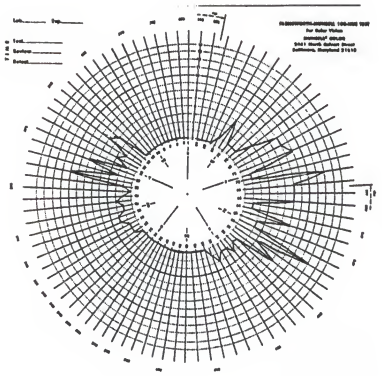


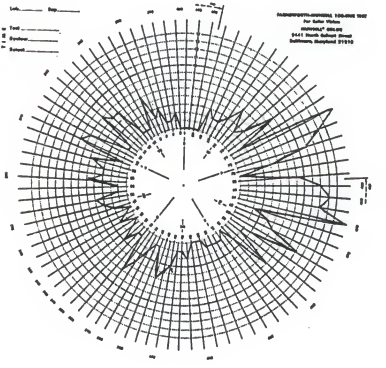


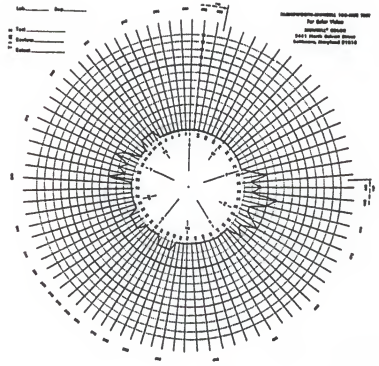


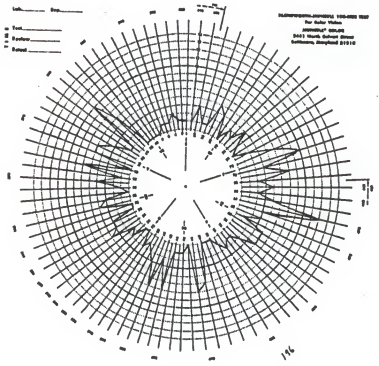


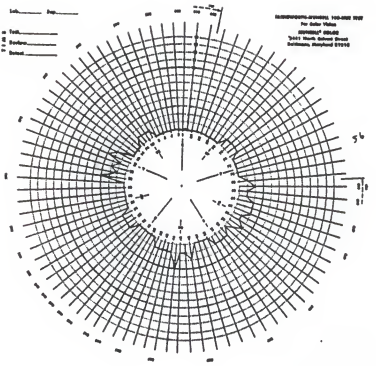


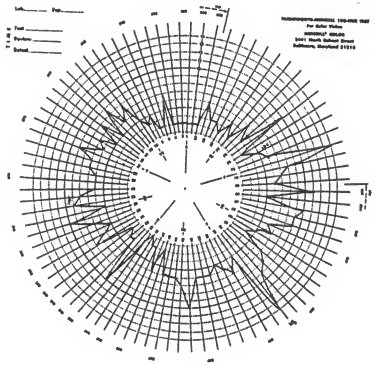


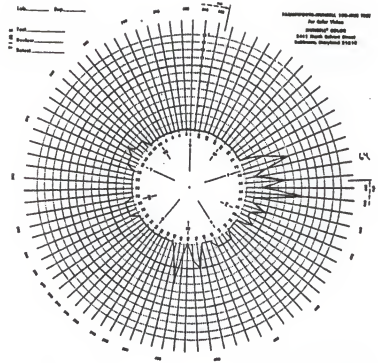


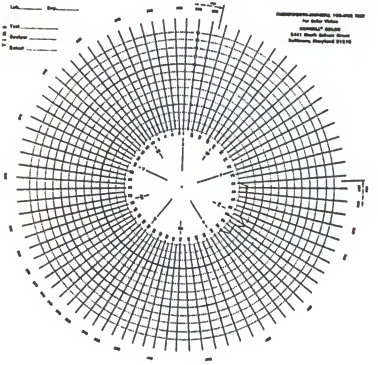


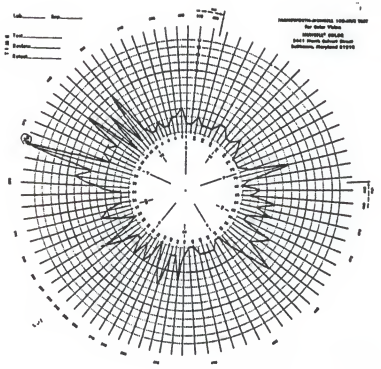


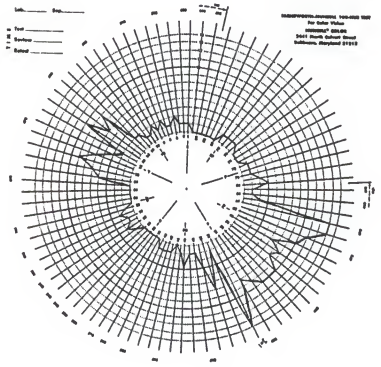


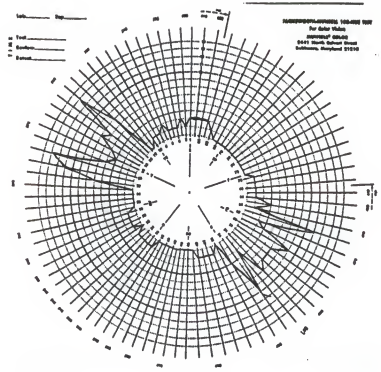


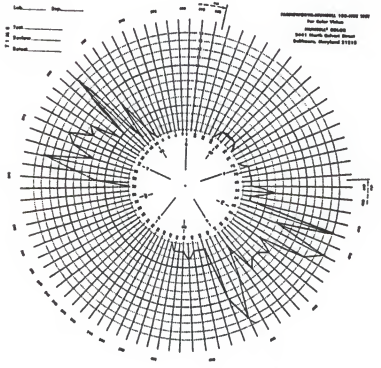


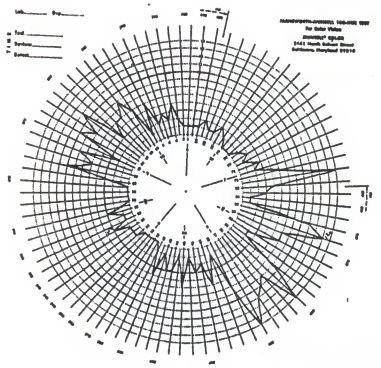


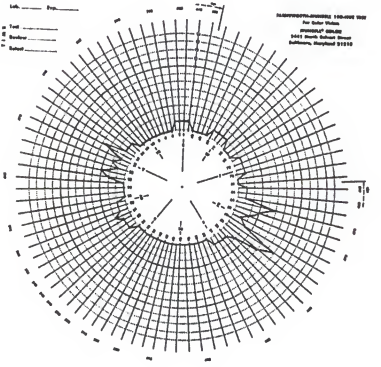


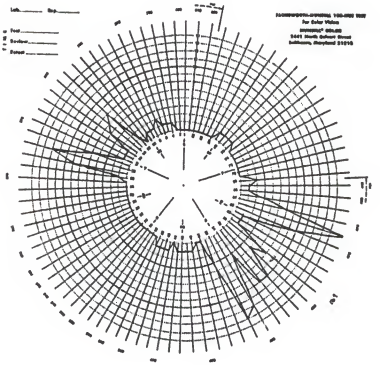


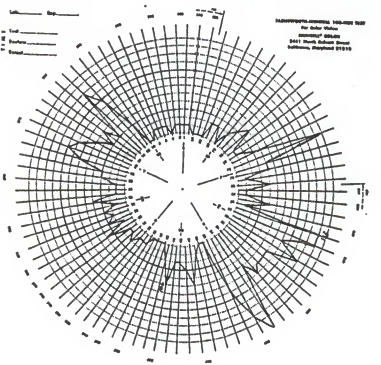


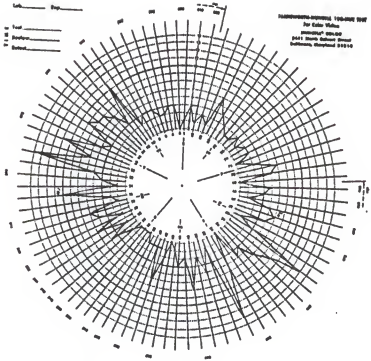


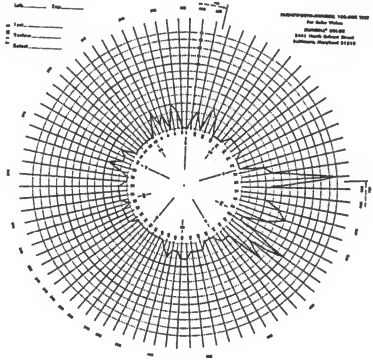


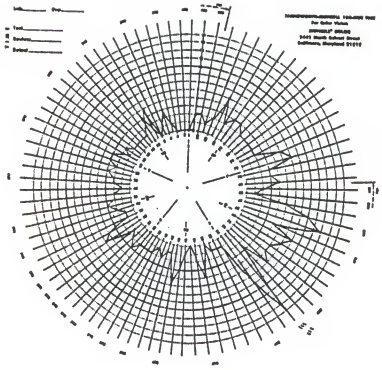












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BIOGRAPHICAL SKETCH

Barrie Woods was born in Spokane, Washington on November 12, 1959 but was raised in Laramie, Wyoming. He attended college there, paying for school by working during the summers as an archaeologist in Taos, New Mexico. He graduated from the University of Wyoming in 1984 with bachelors degrees in Psychology and Anthropology. During his last semester there he took a class entitled "sensory physiology" and knew this was the stuff for him. It was just like you read about: the clouds parted, the angels sang, and C.I.E. illuminant "B" shone down from above.

Barrie came to the University of Florida to study vision in the fall of 1984. He was married in May 1990 during the course of this project.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Keith D. White

Keith D. White, Chair
Associate Professor of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

W. Keith Berg
Professor of Psychology

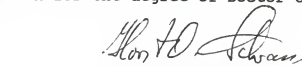
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Ira S. Fischler
Professor of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

David M. Green
Graduate Research Professor
of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Horst Schwassmann
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Howard D. Baker
Professor of Psychology
Florida State University

This dissertation was submitted to the Graduate Faculty of the Department of Psychology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1990

Dean, Graduate School